Biotic Factors Influencing Populations of *Dacus dorsalis* in Hawaii[1]

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INTRODUCTION

The oriental fruit fly, *Dacus dorsalis* Hendel, is widely distributed along the arc from India to Indonesia to Formosa, and in the Mariana Islands. In 1946 it was discovered in Hawaii for the first time and within 2 to 3 years developed into an agricultural problem of major proportions. The devastating effects of the fly on many crops in Hawaii and the potential threat of introduction to the mainland of the United States, led to the establishment of a cooperative research program including agencies of the (then) Territory of Hawaii, the Federal government, private research stations and subsequently the State of California (Clausen, Clancy and Chock 1965, pp. 1–7).

Almost immediate attention was given to the search for natural enemies of fruit flies and many of these were shipped to Hawaii between 1947 and 1951; screened in the laboratory, and released (op. cit., pp. 7–100). In 1949, the Hawaii Agricultural Experiment Station undertook a program to evaluate the effectiveness of the introduced natural enemies of *Dacus dorsalis*.

From the outset it was felt that a program of evaluation of the part played by the introduced enemies could not be carried out without investigation of as many of the factors influencing survival and abundance of flies as could be accomplished feasibly. The work of evaluation was greatly simplified in July of 1950 when *Opius oophilus* Fullaway (Hymenoptera: Braconidae) became the principal parasite of the oriental fruit fly on Oahu and very shortly replaced the others (Van den Bosch, Bess and Haramoto 1951). From the standpoint of parasites, the problem of evaluation, for practical purposes, was thereafter reduced to this one species. None of the established predators or pupal parasites ever became sufficiently abundant to be of any significance in the biological control of the fruit fly. Some of the previously established general predators, in particular ants, were of local importance in certain areas, especially the warm, dry parts of the island.

Opius oophilus is an egg-larval parasite, which oviposits in the eggs of *D. dorsalis*. In the field, females visit and revisit oviposition punctures of

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fruit flies, probing the underlying clusters of host eggs and depositing their own eggs. On the basis of general observations, it appears that multiple parasitization by *O. oophilus* is not common at low levels of parasite activity, but becomes increasingly common at higher levels. The parasite egg hatches at about the same time as the fly egg, and the larva completes its development shortly after puparium formation. The parasitized host forms a normal puparium, but does not pupate; the single adult parasite emerges from the puparium. The egg-larval habit of *O. oophilus* is in marked contrast to that of the other opiine parasites established in Hawaii, all of which oviposit in the larvae of fruit flies (Bess *et al.* 1950).

One of the most illuminating developments of the study was the importance of microorganisms at virtually every stage in the cycle of the fly, although in retrospect, this is perhaps not as surprising as it might seem at first. To begin with, fungi and bacteria are closely involved in the complex interrelationship between the eggs of *Dacus dorsalis* and the ovipositional activity of *Opius oophilus*. This interrelationship contributes significantly to what we speak of as "egg mortality." Egg mortality it is, but it will become apparent that this is not a simple phenomenon; indeed it is the most complex of all the factors investigated since it affects the production of parasites much more directly than it affects the production of flies. Although a major part of our effort was expended in studying this factor, in reality we only opened the door on this most interesting and important phase of the ecology of these insects. In the larval environment, microorganisms again play a dominant role through their effect on larval survival. Adverse effects of microorganisms in the larval environment continue into the pupal and adult stages as well.

It is difficult in some respects to present the results of a study of this type because of the interdigitations of all of the biotic factors influencing populations of *Dacus dorsalis*. For instance, it is impossible to discuss the bearing of fruiting cycles upon fruit fly production without mentioning the important relationship between fruiting cycles and ovipositional activity of the fly, or egg mortality. It is also impossible to discuss the bearing of larval infestation upon production of adult flies without going into the equally important factors of fruit abundance, and the attendant ramifications of true rates of parasitization and of survival of parasitized eggs. To give a true picture of the way that all of these factors are operating in the field, they should all be considered simultaneously, but for practical reasons we can scarcely do this.

The following discussion has been divided into three main sections: (1) factors influencing productivity, (2) factors influencing mortality and (3) evaluation. This is done with the full knowledge that the most important factor influencing productivity is mortality, and if the reader keeps in mind that we realize this, perhaps he will not be too puzzled by the way in which we attempt to construct the 4-dimensional picture of the biotic factors regulating fruit fly populations.

FACTORS INFLUENCING PRODUCTIVITY

Fruiting cycles in guava: It is not possible to understand changes in fruit fly populations without correlating them with fruiting cycles in the major hosts. On Oahu the greater part of the oriental fruit fly population is produced in guava, *Psidium guajava* L., and while there are no figures upon which to base a reliable measure of the production in the various hosts, it is a fairly safe estimate that approximately 95% of the fly population of Oahu is developed in guava fruits. The general population cycles are determined almost entirely by guava fruiting, and probably in only a few cases is fly production in mangoes or papayas heavy enough to markedly influence the population in localized areas. Largely for this reason, we confined our studies on the biotic factors influencing fruit fly abundance to this host.

Because of the great variations in fruit abundance from one part of the year to another, it was essential to have a reliable way of estimating or measuring this factor. Early in the study, we introduced a method of estimating fruit abundance based on yellow-ripe guavas on the trees. The following scale was used, the observations being made, wherever practicable, from a vantage point outside of the area.

0. No ripe fruit evident, even on searching.
2. Ripe fruit present, but found only on searching.
4. Ripe fruit evident without searching, but very light.
6. Ripe fruit moderately heavy on most trees, or a very heavy crop on scattered trees.
8. Ripe fruit everywhere, on nearly all trees, and trees heavily laden.

Numbers 1, 3, 5, and 7 were used in those cases judged to be intermediate between 2 alternatives.

This scale was tested critically in 1951 in 4 gullies near Wahiawa, Oahu, and it was shown that as the estimated *index of fruit abundance* (IFA) increased from 1 to 8, the ground fruits increased from about 0.2 to 50 per 100 square ft, or an increase of roughly 250 times. This relationship is shown in Fig. 1 in which the values are plotted on a numerical scale (right) and a logarithmic scale (left). The values for IFA 6 were considerably out of line because of one unusually high fruit count, but the agreement with a logarithmic curve is generally good. Using corrected values obtained from the logarithmic curve, we can then determine *relative fruit abundance* (RFA) (Table 1). The figures for relative fruit abundance given in Table 1 are average values for numbers of ground fruits per 100 ft^2 in the gullies in which counts were made. Fruit production in these gullies was heavy and possibly somewhat above average for most areas on the island. For any given index, the actual number of ground fruits per unit area probably varies somewhat from 1 guava site to another depending on density of stand and other factors. But with adequate observations, fairly precise estimates of the comparative abundance of fruit at various times of the year, or from

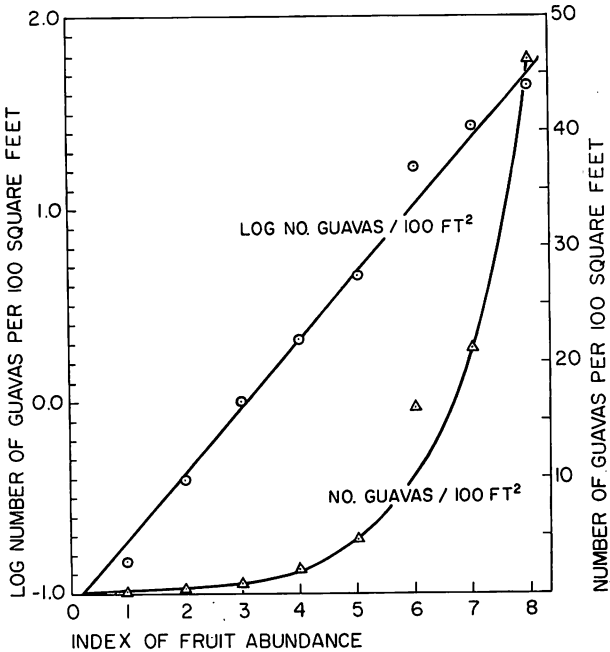

FIG. 1. *Relationship between visual estimates of guava abundance (IFA) and actual numbers of fruits per* 100 *square feet of ground area. Based on data obtained in* 4 *gullies near Wahiawa, August to December,* 1952.

TABLE 1. *Index of fruit abundance (IFA) and relative fruit abundance (RFA) based on visual estimates of yellow-ripe guavas and numbers of fruits on the ground. Values in last line corrected to fit true logarithmic curve. For the particular gullies in which the observations were made, the values in the middle line represent the average number of fruits per* 100 *ft²; for other sites, they are only relative values*

IFA	0	1	2	3	4	5	6	7	8
RFA (obs.)	0.0	0.16	0.60	1.00	2.16	4.66	16.16	21.35	46.40
RFA (corr.)	0.0	0.22	0.47	1.03	2.24	4.87	10.59	23.04	50.12
No. Cases	1	8	14	16	22	10	7	4	1

year to year can be made. Where adequate controls are established, fruit production over very large areas can be estimated in terms of weight or numbers of fruit per unit area.

It is essential to note that comparisons of production in 2 areas or at different times cannot be based on IFA estimates, but only on RFA values calculated from these estimates. To illustrate this, we may compare the fruit production in 2 different partial cycles (Table 2). In the case presented here, the average IFA values for the 2 partial cycles were identical, whereas fruit production in cycle A was actually about 4 times as great as in B. Therefore averages of IFA values have no quantitative meaning and

TABLE 2. *Comparison of estimates of fruit production based on IFA and RFA values, to show invalidity of estimates based on averages of IFA values*

Cycle	*IFA values at successive time intervals*	*Av.*	*RFA values at successive time intervals*	Av.
A	2, 5, 8	5	0.5, 4.9, 50.1	18.5
B	5, 5, 5	5	4.9, 4.9, 4.9	4.9

should never be used for any purpose. Carefully determined average RFA values, however, can be used for direct comparisons of fruit abundance from 1 time to another. For example, the average RFA for the 4 months of maximum spring fruiting for the years 1951 to 1953 was 1.66, while for the fall cycles it was 4.31. The fall crops were therefore about 2.7 times as heavy as the spring crops.

The real criterion for production during a given cycle is not the production during the month of maximum fruiting, but throughout the entire cycle. This was well demonstrated in the 1953 crop when the RFA reached a maximum of 7.3 in October, compared with 6.0 for the same month in 1952. But the RFA averaged only 3.9 over a 4-month period while in 1952 it averaged 5.0, or about 30% greater. The year 1953 was very dry, and this probably accounted for the smaller fruit crop.

The monthly RFA values of the years 1950 and 1953 are given in Table 3. Characteristically there are 2 cycles of guava production on Oahu,

TABLE 3. *Relative fruit abundance, Oahu,* 1950 *to* 1953, *inclusive. Based on estimates made at fruit collecting stations*

	Jan.	*Feb.*	*Mar.*	*Apr.*	*May*	*June*	*July*	*Aug.*	*Sep.*	*Oct.*	*Nov.*	*Dec.*
1950	1.0	0.6	0.3	0.3	1.1	6.8	8.2	10.1	1.5	1.6	2.9	1.2
1951	0.5	0.3	1.7	2.5	0.1	1.4	2.2	3.8	7.8	2.6	1.9	0.2
1952	0.3	3.9	2.2	1.3	1.3	0.3	0.2	0.6	5.3	6.0	5.4	3.1
1953	1.1	1.5	1.5	1.8	1.8	1.4	0.2	0.8	4.3	7.3	2.7	1.3

1 in the spring and 1 in the late summer or fall. Minimum fruit production usually occurs in the months of December, January or February in the winter, and May, June or July in the summer. On the island of Oahu, both the minima and maxima are usually well defined, and very great changes in fruit abundance may occur from 1 month to the next (Fig 3). Throughout the period of study, the spring crop of fruit was always the lighter one, and the quantity of flies produced by it was also smaller despite occasional high rates of infestation.

One of the more important features of fruiting cycles is the relationship between fruit abundance, infestation, and larval populations. A study of Table 4 shows that maximum infestation in the summer or fall coincides with the 1st upswing in fruit abundance following the minimum.

This is a very regular feature of fruit fly populations in general, local variations not withstanding. While infestations in terms of larvae per fruit may be quite impressive at this time the total production of larvae is not as great as in the ensuing months because of the small quantity of fruits. The importance of these early emergents is that many of them may mature in time to attack the guava crop at or somewhat after the peak of fruit abundance.

Maximum production of larvae in all 4 years came the 2nd month after the minimum of fruit abundance. Precisely the same condition was observed in the more detailed study made on Windward Oahu in 1953 (Fig. 7), so it appears that we have here a fairly consistent relationship.

All available evidence indicates that there is a close correlation between fruiting cycles and (1) egg populations, (2) larval populations, (3) adult populations and (4) parasite activity as reflected in true rate of parasitization and egg mortality. These relationships will be touched upon frequently in subsequent sections and will not be discussed further here.

Adult populations: From July, 1950 until December, 1954 we maintained a series of 11 traps on the island of Oahu to obtain a measure of the relative fruit fly population from year to year and season to season. These traps utilized methyl eugenol as an attractant. This compound has a number of properties which make it ideal for the purpose of obtaining a measure of fruit fly populations: it is (1) highly specific for *Dacus dorsalis* males, (2) very stable under field conditions, (3) only moderately volatile and (4) extremely attractive, luring males from distances of some hundreds of yards (Steiner 1952, 1965).

The traps employed in our work were designed to be serviced only once every 30 days or so, and experimental studies showed that they were uniformly effective over periods as long as this. The lure unit was placed in a cubical cage, enclosed on 2 sides by glass, and on 2 sides by screen (Fig. 2). The top of the cage was completely covered, while the bottom opened into a large chamber in which a 5-gallon can was placed. The lure unit (shown on the floor of the trap in the figure) consisted of a short vial with a capacity of about 20 cc. The cork was notched to hold the 2 pieces of blotting paper, which were kept saturated by means of string wicks extending down into the methyl eugenol reservoir.

The lure dispensing vial was held in a rectangular screen cell to keep the flies from drinking the methyl eugenol. The entire lure unit was suspended from the ceiling of the cage. Flies entered the cage through the small holes in either screen, and eventually fell down into the 5-gallon can, where they were caught in flushing oil. Escapes were insignificant, the flies being kept away from the hole in the screen by means of a square collar of galvanized metal 1/2 inch high. Benzoic acid dissolved in the oil prevented decomposition of the dead flies. The flies were collected once a month, and catches were measured volumetrically (approximately 24 flies equal 1 cc).

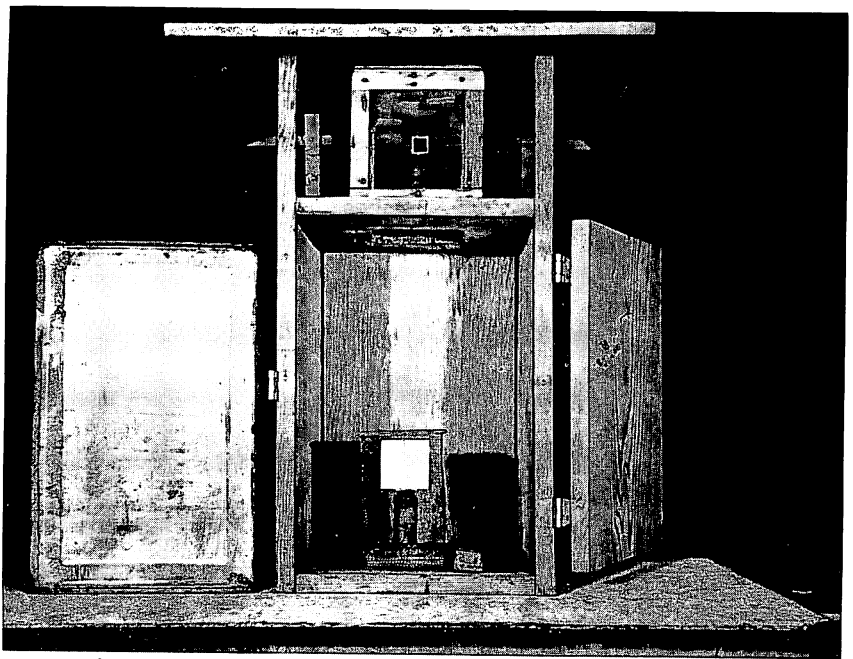

FIG. 2. *Thirty-day methyl eugenol trap used to obtain measure of relative adult populations. The lure dispenser has been removed from the cage. The 5-gallon receptacle is at the left.*

In several of the traps in regions of low catches, it was found convenient to insert an adapter which made it possible to use a 1-gallon can as a receptacle. When the traps were first installed, however, the population was so high that a 5-gallon can was, in some cases, almost inadequate to hold a 30-day catch.

The average catch per day for all 11 traps combined is shown in Fig. 3 and in Table 5. The data on trap catches have been plotted with those on fruit abundance for purpose of comparison. As a rule, the maximum catches occur either 1 or 2 months after peak fruiting. In the case of Fig. 3, the data on fruiting are those from the fruit-collection stations, rather than from the trap stations, and 2 of the peaks coincide. But when trap records were kept in specific areas in which there were well defined fruiting cycles, the maximum catches usually fell from 1 to 2 months after fruiting maxima. In the 30-day trap records, these 2 maxima were almost invariably separated by an interval of either 1 or 2 months, and the mean lag was between 6 and 7 weeks. This was one of the most predictable features of populations of *Dacus dorsalis* in Hawaii.

The last great crop of fruit flies on Oahu developed in the last 1/2 of 1950. That was the year that *Opius oophilus* superseded all other parasites

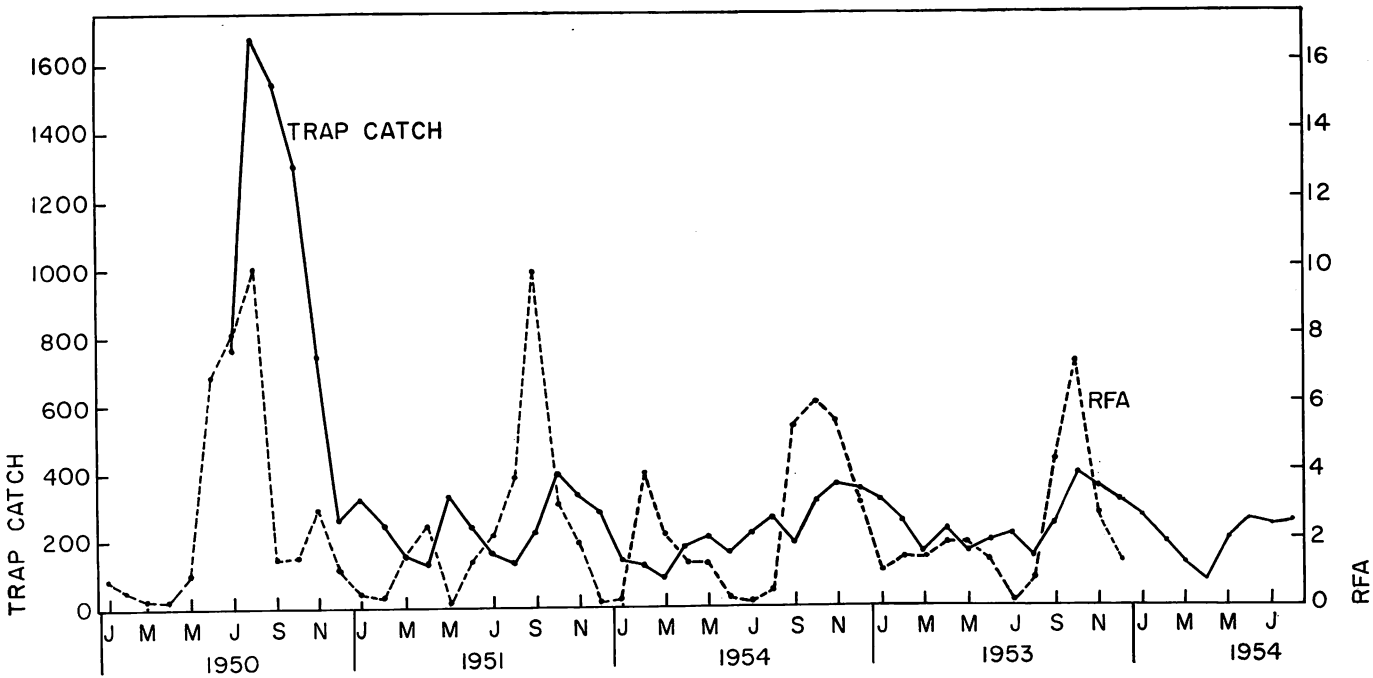

FIG. 3. *Trap catches (solid line) on Oahu, 1950 to 1954. Trap catch in cubic centimeters of ♂ per day for all 11 traps. Relative fruit abundance (dashed line) based on an average of RFA values at each fruit colleection station.*

TABLE 4. *Relationship between initiation of fruiting cycle, maximum infestation, and maximum larval population. The major fruiting cycles for the years of* 1950 *to* 1953 *are superimposed, centered upon the month of minimum fruit abundance immediately preceding the cycle. The position of the figures for minimum RFA (in italics) are therefore arbitrarily fixed, but the others are free to vary*

Year	*Month of Min. RFA*	−2 *Mos.*	−1 *Mo.*	*Min. RFA*	+1 *Mo.*	+2 *Mos.*	+3 *Mos.*	+4 *Mos.*	+5 *Mos.*
1950	April	0.6	0.3	*0.3*	1.1	6.8	8.2	10.1	1.5
1951	May	1.7	2.5	*0.1*	1.4	2.2	3.8	7.8	2.6
1952	July	1.3	0.3	*0.2*	0.6	5.3	6.0	5.4	3.1
1953	July	1.8	1.4	*0.2*	0.8	4.3	7.3	2.7	1.3
	Avs.	1.4	1.1	*0.2*	1.0	4.7	6.3	6.5	2.1
Larvae per fruit									
1950		5.0	8.3	*18.1*	21.9	16.4	7.1	4.5	8.3
1951		1.7	2.1	*5.9*	4.0	5.1	3.4	2.9	1.2
1952		2.7	4.8	*4.7*	10.1	4.4	1.2	0.6	0.4
1953		6.5	7.9	*15.4*	23.8	7.0	2.9	2.2	1.5
	Avs.	4.0	5.8	*11.0*	15.0	8.2	3.7	2.6	2.9
Relative Larval Population (as % of cycle's production in each month)									
1950		2.1	2.6	*1.4*	17.9	32.6	18.5	22.5	2.5
1951		2.3	3.6	*0.5*	20.1	20.7	16.2	32.1	4.0
1952		6.8	4.1	*2.5*	7.0	45.4	19.4	10.2	4.7
1953		8.6	4.4	*2.6*	15.4	48.2	15.7	3.5	1.6
	Avs.	5.0	3.7	*1.7*	15.2	36.7	17.4	17.1	3.2

of *Dacus dorsalis* on Oahu. The effects of this heavy emergence extended into the first 1/2 of 1951, but fly catches the last 1/2 of that year, and especially the first 1/2 of 1952, were at an all-time low. The following 12 months, however, saw an increase of about 28% in average daily catch of flies. There is no reasonable doubt that this represented a partial release from the effects of *Opius oophilus*. The increase was associated with somewhat lower rates of parasitization which were first observed in November 1951 and extended well into 1952. In fact, no subsequent 6-month period has shown a sustained rate of parasitization equal to that which existed during the last 1/2 of 1951. The trap collections were continued by Bess and Haramoto (1961, p. 20) from 1954 to 1956 and showed no marked variation from the level reached in 1953.

The relationship between adult populations and productivity is not an easy one to evaluate, because there is no simple way to differentiate between gross population size and the size of the reproducing population. Those large populations which appear after peaks of host abundance are obviously composed principally of young adults, most of which do not immediately engage in egg-laying activities. The reasons for the latter are not clear, but the evidence is unmistakable, and comes from various

independent observations. In any area in which there is a well-defined fruiting cycle, the maximum catches of flies are usually made after the maxima of fruit and egg production have passed, and not coincidentally. This was clearly shown in the course of a study in an isolated gully at Wahiawa in 1951 in which the relative numbers of fruits, eggs, larvae and adults were measured throughout a complete fruiting cycle. In Fig. 4 it is seen that the maximum of fruit abundance (determined by actual counts of fruits on the ground) was reached 10 October, while peak egg and larval populations were observed a week later (these actually may have occurred 10 October also, but no fruit collections were made on that date). The adult male population rose moderately throughout the first 6 or 7 weeks of the cycle, quite certainly reflecting the accumulation of a breeding population in response to the presence of fruits. But the highest catches of all were recorded 21 November, 6 weeks after the fruit maximum and 5 weeks after the egg and larval maxima. This clearly represented the emergence of a new crop of adults.

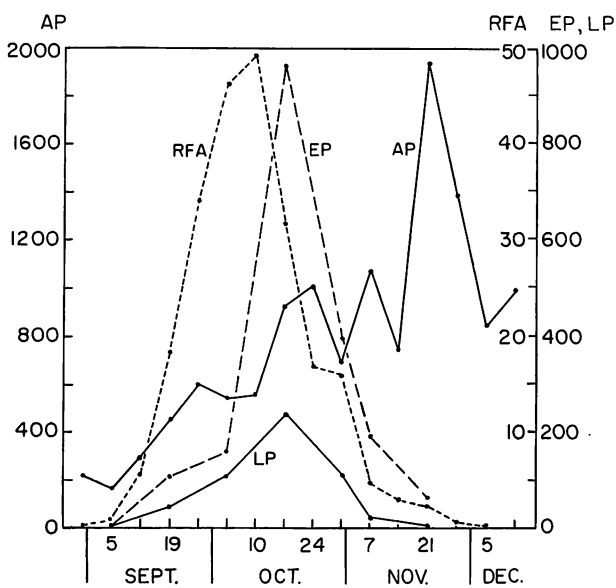

FIG. 4. *Relationship of egg (EP), larval (LP) and adult (AP) populations to cycle of fruit abundance (RFA), based on data from gully at Wahiawa,* 1952.

The significant feature about this cycle with respect to the relationship between adult populations and productivity is that the ovipositional activity was many times greater around 17 October than it was on 21 November, at the peak of the fly population. The actual number of eggs produced was roughly 15 times as great on the former date, and these were laid by only 1/2 as many flies as were present on 21 November. Combining these

2 values, the flies present in the gully on 17 October were producing eggs at about 30 times the rate of those on 21 November. Even the number of eggs per fruit on the earlier date (30.6) exceeded that on the later date (26.1). It is necessary to conclude, therefore, that large populations of adult flies do not, in themselves, mean high ovipositional activity. On the contrary, the highest adult populations ordinarily occur at a time when egg production is at a very low point. Maximum egg production occurs at times of increasing or maximum fruit abundance and the fly populations present at such times are usually of only moderate size. They appear to comprise flies which for the most part have survived in the field for considerable periods of time and which become concentrated in areas in which there is a maturing crop of fruit. Declining fruit crops are paralleled by declining ovipositional activity.

TABLE 5. *Average catch per day in 11 methyl eugenol traps on Oahu, 1950 to 1954. Measurements in cubic centimeters*

Monthly

Year	*Jan.*	*Feb.*	*Mar.*	*Apr.*	*May*	*June*	*July*	*Aug.*	*Sep.*	*Oct.*	*Nov.*	*Dec.*
1950	—	—	—	—	—	—	776	1640	1539	1297	744	268
1951	313	261	158	129	334	245	162	148	216	395	327	196
1952	143	130	93	186	202	167	214	270	191	313	362	346
1953	312	260	171	226	170	195	221	146	255	393	351	305
1954	271	187	128	77	198	252	235	243	322	314	239	175

Quarterly

	Jan.-Mar.	*Apr.-June*	*July-Sep.*	*Oct.-Dec.*
1950	—	—	1318	770
1951	244	236	175	306
1952	122	185	225	340
1953	248	107	207	353
1954	195	176	267	243

Oviposition and egg populations: The eggs of *Dacus dorsalis* are nearly always deposited in clusters lying between 1 and 3 mm below the surface of the fruit. In guava fruits, the tissues exhibit a typical reaction at the site of a sting, drying and shrinking away from the eggs somewhat. This reaction is often more marked when the egg lesion is infected by fungi introduced by the ovipositional activity of the fly or parasites, or less commonly by mites of the family Acaridae. One important feature of *D. dorsalis* is that, like many other species of Tephritidae, it characteristically oviposits in old lesions. This is probably of considerable significance in the matter of egg mortality induced by *Opius oophilus* as will be explained later. Another important factor in the bionomics of the fly is that the eggs are virtually beyond the reach of natural mortality factors, with only the one exception of *Opius oophilus*. Numerous observations show that the natural rate of hatching in eggs in the field is extremely high, approaching 100%,

when field-reared flies are used and when parasites are excluded.

Excepting abortive lesions containing no eggs, the number of eggs per sting ranges from 1 to more than 100. Of several 1,000 lesions examined from 1950 to 1953, only 3 had more than 100 eggs (101, 109 and 127, respectively), and all but a very few yielded fewer than 70 eggs. Lesions containing 6 to 12 eggs outnumbered those containing 1 to 5, or 13 to 18, etc. All stings combined yielded an average of 13.5 eggs per sting.

Ovipositional activity, as measured in terms of eggs per sting, showed appreciable regional differences. Thus, 72 samples from various points in the broad central valley on the west (leeward) side of the Koolau range averaged only 10.7 eggs per sting; while 103 samples from the east (windward) side of the range, and the "mauka" or montane fringes of Honolulu averaged 15.5 eggs per sting. The significance of this is reflected further in the number of fruit fly lesions per fruit, which averaged only 1.7 in the central portion of the island, but 2.9 in the samples from the northeastern and southern fringes of the Koolaus.

During the course of the evaluation studies it was observed that at any given point a large increase or decrease in the number of stings per fruit was nearly always associated with a corresponding increase or decrease in the number of eggs per sting. The same relationship is revealed when all data are pooled without regard to locality or season. Therefore it is apparent that any marked increase in intensity of oviposition, whether arising from increased number of ovipositing females or from sharp reductions in fruit abundance[4], leads not only to more frequent attacks on the individual fruits (as indicated by the number of stings per fruit), but also to more frequent visits to the old lesions (as indicated by the number of eggs per lesion). It is possible that there is a corresponding increase in number of eggs laid per oviposition, but there are no data to prove or disprove this.

It should be apparent from the above that any changes in these 2 factors will be associated with even more marked changes in the number of eggs per fruit. For example, if there is a doubling of both factors, the number of eggs per fruit will increase by 4 times, etc.

With accurate estimates of fruit abundance and the number of eggs per fruit, it is possible to obtain a useful measure of relative egg populations. The time required for egg counts almost prohibits such measurements over very large areas, but in the last 1/2 of 1953 the relative egg population was determined for Windward Oahu, from Punaluu to Nuuanu. This area of about 75 square miles produces more fruit flies than any other portion of the island of comparable size. The results of this study are corroborated by numerous other observations, and, considering the large area covered,

[4]It must not be inferred from this that periods of low fruit abundance are characterized by intensive concentration upon the few fruits present. On the contrary, periods of *minimum* fruit abundance are typically correlated with minimum ovipositional activity. Immediately following the fruit maxima, there is often a moderate, temporary increase in the number of eggs per fruit, but this is never in proportion to the decrease in fruit abundance.

they must be fairly typical of the island as a whole. The methods and results are given in greater detail in the section on egg mortality and in Fig. 7. Here it will simply be pointed out that the curve for egg abundance has almost precisely the same form as that for fruit abundance, regardless of the number of eggs per fruit. This follows from the observed fact that, over large areas such as the one studied here, the minimum number of eggs per fruit seldom differed from the maximum by a factor of more than 1 : 2 while changes in fruit abundance are more often of the magnitude of 1 : 10. As a result, egg populations are determined more by fruit abundance than by numbers of eggs per fruit.

Another example of the close relationship between fruiting cycles and egg populations is shown in Fig. 4. The correlation in this case may actually have been better than shown had egg counts been made at the peak of fruit abundance on 10 October. The bearing of egg populations upon larval populations will be treated further in the section on egg mortality.

Larval infestation and populations: The magnitude of the larval population depends upon 3 main variables—fruit abundance, the number of eggs per fruit, and the percentage hatch of the eggs. The latter in turn depends upon the size of the parasite population relative to the egg population and probably upon epizootic factors as well, namely, the incidence of infection in the egg population. As pointed out in the section on fruiting cycles, the most favorable combination of these factors in large populations is found about 2 months after the fruiting minimum, 1 month after the maximum larval infestation and either coincident with, or a month or so prior to the peak of fruit abundance (Table 3 and Figs. 4 and 7). Usually at the time of maximum larval populations, egg mortality has risen to such a high level that further increases in fruit abundance or number of eggs per fruit are insufficient to offset the decrease in percentage hatch, and the larval population consequently falls. This appears to be the general picture when populations over large areas are concerned.

The monthly records for larval infestation are given in Table 6. In studying this table it must be remembered that the figures for 1953 cannot be compared directly with those for the earlier years, because of modifications in techniques necessitated by changes in personnel and the scope of our research program. The data from 1949 through the first 10 months of 1951 are from the collections made by Robert Van den Bosch in connection with the recovery and spread phase of the program. The size of the samples varied considerably, ranging from 1 to as many as 50 and more guavas. In November 1951 we restricted our samples to a maximum of 20 fruits at each station. The same 40 stations were retained. This program was continued through 1952, but in 1953 the entire fruit sampling program was revised. The 5 stations in the Kunia-Schofield area were discontinued and an additional 25 stations on the Koolau side of the island were selected, making a total of 60 stations in all. At each of the stations, only 4 fruits

TABLE 6. *Number of larvae per fruit, Oahu,* 1949 *to* 1953. *The* 1953 *values cannot be compared directly with the other years because of changes in technique described in text*

	Jan.	*Feb.*	*Mar.*	*Apr.*	*May*	*June*	*July*	*Aug.*	*Sep.*	*Oct.*	*Nov.*	*Dec.*
1949	—	—	—	—	—	—	—	—	—	—	12.4	7.0
1950	3.6	5.0	8.3	18.1	21.9	16.4	7.1	4.5	8.3	4.4	1.1	0.4
1951	0.3	2.4	1.7	2.1	5.9	4.0	5.1	3.4	2.9	1.2	1.0	1.5
1952	0.8	4.4	3.0	1.9	2.7	4.8	4.7	10.1	4.4	1.2	0.6	0.4
1953	1.7	3.2	4.5	5.7	6.5	7.9	15.4	23.8	7.0	2.9	2.2	1.5

TABLE 7. *Variation in numbers of larvae in each of* 4 *subsamples. Four fruits per station,* 60 *stations, Oahu,* 1953

Subsample	*Jan.*	*Feb.*	*Mar.*	*Apr.*	*May*	*June*	*July*	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Dec.*
A	60	153	200	205	306	350	634	1158	426	171	144	56
B	88	127	166	245	230	411	703	1222	425	180	166	98
C	105	201	205	210	322	446	717	1056	384	162	113	59
D	95	167	216	314	329	321	614	1128	412	165	85	52
No. Fruits/ Subsample	51	51	44	43	46	48	43	48	39	59	57	44
		A			B			C			D	
Year Total		3863			4061			3980			3898	

per month were collected, when available.

The 4 fruits at each station were distributed among 4 subsamples in order to provide a check on the reliability of the entire sample. The fruits were retained in the order collected, and then distributed among the 4 subsamples according to a predetermined schedule of rotation involving all the possible sequences, in order to eliminate any unconscious selection. The total number of larvae in each of the 4 subsamples for each month is shown in Table 7. The variation between subsamples is small enough that the 4 subsamples combined would appear to give a fairly reliable estimate of larval infestation for each month. The yearly totals for each subsample, reduced to terms of larvae per fruit give values of 6.7, 7.1, 6.9, and 6.8 larvae per fruit, so that the estimate based on the combined subsamples would seem to leave very little to be desired.

The method of handling the fruit was also changed. Previously the guava fruits were discarded after they were dissected and the visible larvae removed. With only 4 fruits per station, however, it was possible to hold the remains of the dissected fruits in pans and make recoveries of all larvae missed in the first dissection. This minimized any variability due to differing recovery rates, or age stratification of the larvae, and also made the entire sampling procedure more reproducible, since operators with even widely varying degrees of dexterity in finding larvae at the first dissection would eventually come out with virtually identical values for infestation.

The dissected fruits at all times were maintained under conditions most favorable to larval survival, being well drained in the early stages of breakdown of the fruit and piled together to conserve moisture as the fruits became drier.

It was realized at the time these changes were instituted that the results would not be comparable with the earlier infestation data, but it was necessary to make the alterations in order to continue other phases of the work. Furthermore, the data would provide a basis of reference in evaluating any future changes in infestation. The results were at least as reliable as those from the earlier collections, since sampling was more widely spread and several sources of variability were eliminated. The increase in number of stations also resulted in a better estimate of fruit abundance. The time required was greatly reduced.

This small sample technique (Newell 1957) does limit somewhat the possibility of making comparisons between localities, but this is not a serious defect. Actually, the 60 stations were divided into 4 regional sections, 1 section of stations being collected in 1 day. Section 1 included the central windward Koolaus, from Punaluu to Nuuanu, Section 2 the southeast end of the Koolaus, from Kailua to Manoa, Section 3 the central leeward Koolaus, from Tantalus to Waikakalaua, and Section 4 the northern leeward Koolaus from Wahiawa to Waimea. Sections 1 and 2 showed highly significant differences from 3 and 4 in infestation. The average of 12 monthly values were 10.5 and 9.0 larvae per fruit for sections 1 and 2 compared with 3.3 and 4.5 for sections 3 and 4. More confidence can be placed in the importance of these differences than in the differences between, say, 2 individual guava groves, so that little is really lost in the way of being able to compare different portions of the island.

Unfortunately we do not have a record of this kind going back to the beginning of the outbreak of *Dacus dorsalis*, covering fruit abundance, larval infestation, and percentage of parasitism, for with these 3 variables measured, it would be possible to make very reliable estimates of larval and adult production and these figures would be of utmost value in evaluating just what has been taking place in the fruit fly population.

Factors Influencing Mortality

Egg Mortality

During the latter part of 1950 it was observed that egg lesions in guavas on Oahu frequently were densely packed with fungi and that a large proportion of the eggs were dead. Whether or not this was a recent development or a condition of some standing could not be ascertained directly, for no detailed studies of the egg lesions of *Dacus dorsalis* had been made previously. Since this was obviously an important source of mortality in the fruit fly population, studies were initiated to determine its incidence and causes in the field.

Methods: In egg mortality studies, mature yellow tree fruits were picked and wrapped carefully in clean paper towels. In the laboratory, they were unwrapped and held in individual jars for at least 1 day, and usually 2. It was found advisable to dip them in 0.5% copper sulfate or copper acetate to which a small amount of detergent had been added. This did not affect hatching, but did retard deterioration of the fruit by fungi. In dissecting the fruits, the skin was scored lightly with a scalpel, being marked in quadrants to facilitate search for the egg punctures. Most of these could be seen readily, but some of the smaller ones required very close scrutiny under the dissecting microscope. The data recorded for each sting included (a) number of eggs, (b) number of eggs obviously dead, (c) whether or not hatching had occurred and (d) any other pertinent information. If heavy hatching had occurred the lesions were frequently eaten out and the dead eggs or chorions scattered. In such cases, the eggs or chorions seen were tallied and the tally marked with a circle. The larvae were removed to blended papaya medium. No attempt was made to associate larvae with stings, but only with the individual fruits. The dissected fruits were then held and recoveries made until all larvae had been removed. For each fruit, the total egg count was taken as either (1) the actual number counted, or (2) the number of obviously dead eggs plus the number of larvae, whichever was the greater. This adjusted value for total eggs was often necessary in fruits in which the hatch was exceptionally heavy, but only rarely in fruits in which the hatch was normal. The hatch was determined by dividing the number of larvae by the number of eggs. A true understanding of changes in fruit infestation and fly population is totally impossible without a knowledge of the role of egg mortality.

Incidence in field: From late 1950 until 1952, about 175 samples of tree fruits collected at various points on the island of Oahu were studied. In these the mortality ranged from 4 to 100% and averaged 76.1%. This average was undoubtedly a little low for the island as a whole and for all seasons during the period, since some of the samples were from areas specifically selected for investigation of heavy infestations. The majority of samples were taken in connection with other phases of the study, however. A total of 61,898 eggs recorded in this study produced 10,832 larvae, for a mortality of 82%. The overall mortality of eggs in guavas on Oahu during these 2 years probably lay at about 80 per cent.

In Fig. 5 the data from these studies have been summarized in graph form to show the distribution of the 175 samples according to the percentage of egg mortality. A study of this graph shows that 7 out of 10 samples had an egg hatch less than 30% and, in 1/3 of all samples, fewer than 10% of the eggs hatched. However, hatching in the field is potentially capable of being as high as that obtained in the laboratory under the most favorable conditions; in 12 samples the hatch was in excess of 70% averaging 88%,

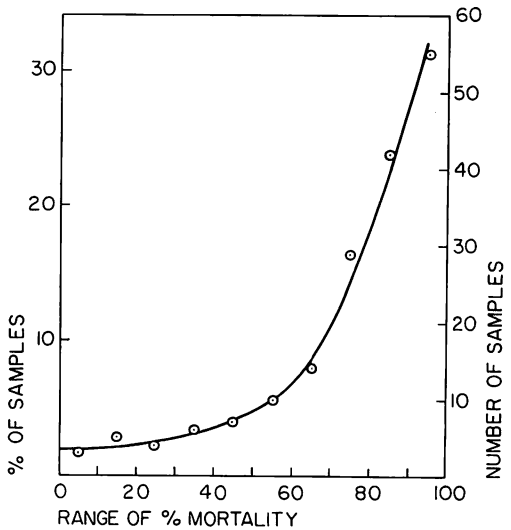

FIG. 5. *Number and percentage of samples with* 0 *to* 10%, 10 *to* 20%, 20 *to* 30%, *etc., egg mortality. Based on* 175 *samples collected from late* 1950 *through* 1952, *on Oahu.*

even though 80% of all the eggs in these samples were parasitized. In one sample of 20 fruits, 96% of a total of 91 eggs hatched.

The sampling was not designed to detect either seasonal or local differences in egg hatch. When all data on egg hatch are arranged according to month of year, it is seen that there are 2 maxima, one in March and 1 in August (Table 8). These 2 months were also the ones in which maximal or submaximal larval infestations were observed not only in the special egg mortality samples, but in the general fruit collections as well, and there is no doubt that there is a causal relationship between low egg mortality and high infestation. It should also be noted that there is a poor correlation between the trends in number of eggs per fruit and larvae per fruit,

TABLE 8. *Seasonal differences in egg hatch based on* 175 *samples from Oahu,* 1951-1952, *and relationship to other factors for same* 2*-year period. Data on larvae per fruit* (*b*) *and* % *of reared larvae parasitized* (% *Par., R.*) *based on* 2 *years collecting from regular fruit sampling stations. RFA based on an average of the estimates from fruit stations, trap stations, and egg mortality stations, combined*

Month	*Jan.*	*Feb.*	*Mar.*	*Apr.*	*May*	*June*	*July*	*Aug.*	*Sep.*	*Oct.*	*Nov.*	*Dec.*
% Hatch	7.2	27.1	54.2	18.0	9.2	19.0	16.8	30.8	18.1	15.4	9.2	14.4
Larvae/Fruit (a)	2.8	7.0	10.0	5.9	8.8	11.4	12.3	9.4	3.4	4.1	3.2	1.2
Eggs/Fruit	38.4	25.9	18.7	32.7	96.5	60.0	73.3	30.6	18.5	26.6	34.4	8.2
Larvae/fruit (b)	0.6	3.4	2.4	2.0	4.3	4.4	4.9	6.8	3.7	1.2	0.9	1.0
% Par., R.	83	67	61	74	79	76	82	74	77	79	72	83
RFA	0.6	2.3	2.7	2.8	2.6	0.9	1.0	2.2	5.9	6.1	3.4	1.4

which again suggests that egg mortality is the controlling factor here and not ovipositional activity on the part of the flies.

Causes of egg mortality: A number of possible causes of natural egg mortality were considered, the more probable ones investigated being (1) traumatic injury by the egg-larval parasite, *Opius oophilus*, (2) pathogenic fungi and bacteria transmitted by flies or (3) by parasites, (4) "corking off" of egg lesions by guava fruits, (5) microorganisms acting independently and (6) infertility of eggs stemming from nutritional or other causes.

The last 2 of these were definitely eliminated as significant sources of mortality by numerous experiments. First, it was shown (by interspersing freshly-laid viable eggs with fungus and bacteria-ridden eggs from the field in moist-chamber preparations) that viable eggs would hatch even when placed in direct contact with dead eggs removed from moldy lesions in guava, and this despite vigorous growth of fungi and bacteria. No significant mortality was ever observed in experiments of this type. Therefore, the microorganisms involved are not capable of invading intact viable eggs. Second, it was shown by capturing ovipositing females in the field and rearing them in the laboratory that the vast majority (about 98%) of eggs laid by these females were viable. Furthermore, flies captured on fruits in the field appeared to be laying at maximal rates. When kept in the laboratory on a diet of sugar and water, the oviposition rate fell off rapidly until at the end of 5 days the flies were laying at only 10% of their output of the first day. Addition of soy hydrolysate to the diet led to accelerated egg production, but this did not quite attain the output of the same females on their 1st day in the laboratory. Therefore, it appears that adult fruit flies in the field are getting adequate nutrients to assure both a high rate of egg production and a high rate of fertility and viability.

The possibility that egg mortality is caused by pathogens transmitted by ovipositing females of *Dacus dorsalis* is eliminated by experiments in which field-captured flies were permitted to oviposit in growing guava fruits in the field. In no case was any significant mortality of eggs observed and the hatch always approximated 100%. These same tests also effectively eliminated "corking off" as a possible cause of egg mortality. While certain host fruits appear to be capable of enclosing the egg lesions in a fibrous case and thus preventing infestation, this is definitely not true in guavas, even when growing on the tree. Although some heavy "corking off" does occur in guavas, it is evidently in response to the presence of microorganisms rather than to eggs of *Dacus dorsalis*, and it does not inhibit infestation to any extent. Egg lesions that show little evidence of fungus infection also show little hardening of the walls[5]; moreover, no cases have been

[5]A type of host reaction usually observed in clean egg lesions in guava is a shrinking and drying of the surrounding tissue, which also becomes straw yellow or light brown in color. This occurs within 24 hours or so after oviposition and could be a normal defensive reaction on the part of the host which inhibits invasion of the rest of the fruit by bacteria or fungi. However, the tissues do not become indurated and do not provide a barrier to larval invasion. Induration seemingly occurs only in the presence of fungi and bacteria.

observed of larvae trapped within a hardened lesion in guava, aside from exceptional individuals which might have been weak to begin with. No more than 1 or 2 dozen such larvae were observed in 3 years.

By elimination, we are left with only 2 of the possibilities considered above, namely traumatic injury by *Opius oophilus* and infection by microorganisms introduced by that parasite. The evidence for the involvement of *Opius oophilus* is irrefutable, but it is difficult to say which of the 2 factors is the more important. It seems quite certain that both are involved, however. What makes it so difficult to differentiate between them is that their effects are largely parallel —the more trauma, the greater the likelihood of infection, etc. At the same time, their effects cannot be equated completely, for conditions other than trauma, namely the incidence of infection in the egg population, may also have a pronounced effect on egg mortality. This is difficult to prove, however, and the only evidence we have to date is of a circumstantial nature.

True percentage of parasitization: At this point it is well to emphasize that all the lines of evidence lead to the conclusion that a dead egg in a normal guava lesion is a parasitized egg. It is necessary to make this assumption in egg mortality studies, since it is impossible to examine each dead egg separately. Moreover, failure to detect a parasite egg or larva by no means proves that a given fly egg was not parasitized. Many dead eggs are so heavily packed with microorganisms that it would be impossible to detect even a well sclerotized parasite head capsule. The number of parasitized eggs in a given sample can be calculated by the following formula: Eggs parasitized = Dead eggs + (No. Larvae x % *Opius* reared from puparia). The systematic errors inherent in the above assumption appear to be negligible.

It is also necessary to establish the important difference between 2 parameters of parasitization. When speaking of the % of parasitization, it is customary to think in terms of the % of fruit fly puparia producing parasites. Thus, if 100 puparia collected under natural conditions produced 75 *Opius oophilus* and 25 *Dacus dorsalis*, we would say this represented 75 % parasitization. But, if this were an average sample, these 100 individuals would have represented the product of a minimum of 500 eggs. Four hundred (80%) of the eggs would have died without hatching, and the remainder, assuming no mortality whatever in the larval and pupal stages, would have matured to adults. The actual number of eggs required would exceed 500 by whatever factor necessary to compensate for larval and pupal mortality and this would be determined by the conditions of rearing. Moreover, in order to inflict a mortality of 80% of the eggs, experience shows that on the average 95% of all the eggs must have been parasitized by *Opius oophilus*. Therefore, an average sample which produced 75% *O. oophilus* and 25% *Dacus dorsalis* would represent not 75% parasitization, but actually 95%. It is therefore imperative to differentiate clearly be-

tween % of parasitization as determined by rearing, and true % parasitization. This distinction will be implicit at all points in subsequent discussion whether stated or not.

The relationship between true % parasitization and egg mortality is shown in Fig. 6, which is based on the samples collected from November 1950 through 1952. This shows only that portion of the curves for which the most reliable data are available. The data from the samples were first grouped according to the % of eggs parasitized and then the total numbers of eggs, larvae, parasites and flies produced in each group were calculated, From these totals, The % mortality of parasitized eggs and the % parasitization by rearing were determined for each group.

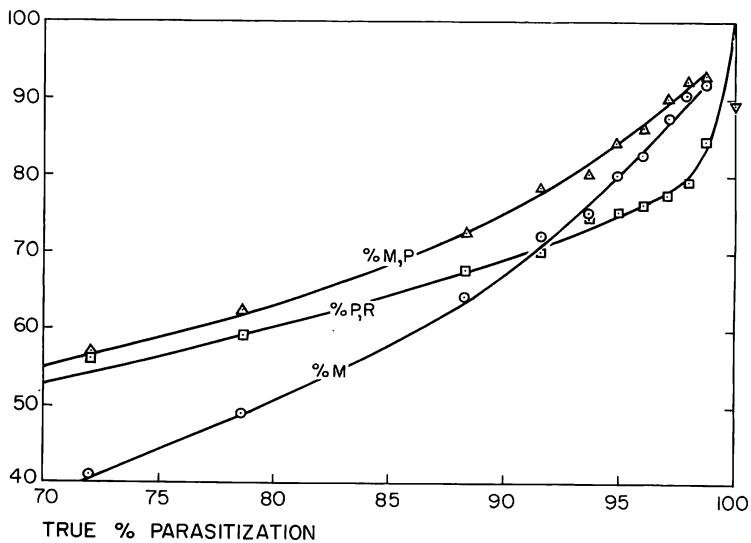

FIG. 6. *Relationship of true* % *of parasitization of eggs (horizontal scale) to the factors of* % *mortality of the parasitized eggs* (% *M, P*), % *mortality of all eggs* (% *M*), *and the* % *of* Opius oophilus *emerging from the reared larvae (vertical scale). Based on* 175 *samples from Oahu, nearly all collected in* 1951 *and* 1952.

As the % of eggs parasitized falls from 100 the mortality falls at a much more rapid rate, reaching a level of about 38% mortality when 70% of the eggs are parasitized. This means that slight changes in degree of parasite attack can produce relatively great changes in egg mortality (or hatch). Generally speaking, these fluctuations are due to differences in hatch of eggs rather than to differences in the number of eggs per fruit. This is well illustrated by the 1953 guava cycle on Windward Oahu, discussed below.

The % mortality of the *parasitized* eggs also declines with decreasing degree of parasite attack, but at a slower rate than the overall egg mortality. When 98% of the eggs are parasitized, 92% of these parasitized

eggs die; when 70% are parasitized, 55% of the parasitized eggs die.

One phenomenon for which there is no certain explanation at present is the mortality in those samples in which 100% of the eggs are parasitized. It might be expected from an extrapolation of the curves in Fig. 6 that the mortality in these would be approximately 96 or 97%. However, the observed mortality (based on total eggs and total larvae) was only 89 % in that group of samples in which all eggs were parasitized. While this does not agree with what might be expected, the data in this portion of the graph are too extensive to dismiss this as a chance variation. Both points are indicated by the single inverted triangle in Fig. 6, but are not joined to their respective curves (at 100% parasitization, the values for % mortality and % mortality of parasitized eggs are necessarily identical).

One possible explanation lies in the complex relationship between degree of parasite attack, microorganisms and fruiting cycles. In an egg population already sustaining 95% true parasitization, further parasite attack will only serve to further increase the rate of true parasitization and mortality. But at 100%, any further parasite attack will increase only the mortality, while the true % parasitization must necessarily remain the same. Now in egg populations already sustaining 100% true parasitization and very high egg mortality, any lessening of this degree of parasite attack would result first of all in a lessened mortality, with no decrease in the true % parasitization. If we add to this the seeming likelihood that in a small but expanding egg population the incidence of infection by bacteria and fungi is reduced because of less frequent revisitation of old lesions and previously parasitized eggs, then it is to be expected that great variations in the degree of hatch will occur. Theoretically these variations should be greater in the range of 100% true parasitization than at any other level, for a decrease in parasite attack at the other levels will usually lead directly to a decrease in the true % of parasitization. In the field, maximum rates of egg parasitization and mortality are usually encountered in the intervals between fruiting cycles when fruit abundance and egg populations are very low. At the beginning of a new cycle, there is a small but progressive increase in the egg population, which at first is usually small enough for the parasites present to cope with. They may even be able to continue to parasitize all the eggs for a while, but superparasitization and the rate of revisitation of old, infected lesions, is reduced and consequently egg mortality is also reduced; sometimes very greatly so. This will be treated further in the section on microorganisms and egg mortality. The data in Tables 9 and 10, and the accompanying text are especially important in this connection.

Egg mortality and egg and larval populations: Because of the time required by egg counts, it is difficult to determine egg populations for a very large area. In fact, if statistical reliability at each observation point is insisted upon, it becomes virtually impossible to obtain results which are

of general application because of the necessary limitation in number of points studied. However, the use of small sample techniques, in which point-reliability is sacrificed for greatly extended coverage, produces results which can be both statistically reliable and of general applicability.

In 1953 a study of the relationship between fruiting cycles, egg abundance, and egg mortality was undertaken on the windward side of Oahu. Two fruits per month were collected at each of 14 stations during the months of August to December inclusive, which covered the fall crop of guava. This area is a relatively uniform continuum with respect to the factors of fruit abundance and infestation, and the 28-fruit samples each month undoubtedly provided a fairly accurate picture of the variables which were studied.

The results are shown in Fig. 7. Fruit abundance was minimum in July when the RFA averaged 0.2, to which point it had fallen from the spring maximum of 1.5 in April. Infestation in terms of larvae per fruit showed a distinct unimodal trend throughout the year —there was no spring maximum, but only a fall maximum in August. This followed just 1 month after the low point in fruit abundance had been reached. Such a pattern was so typical throughout the 4 years that close studies of fruiting

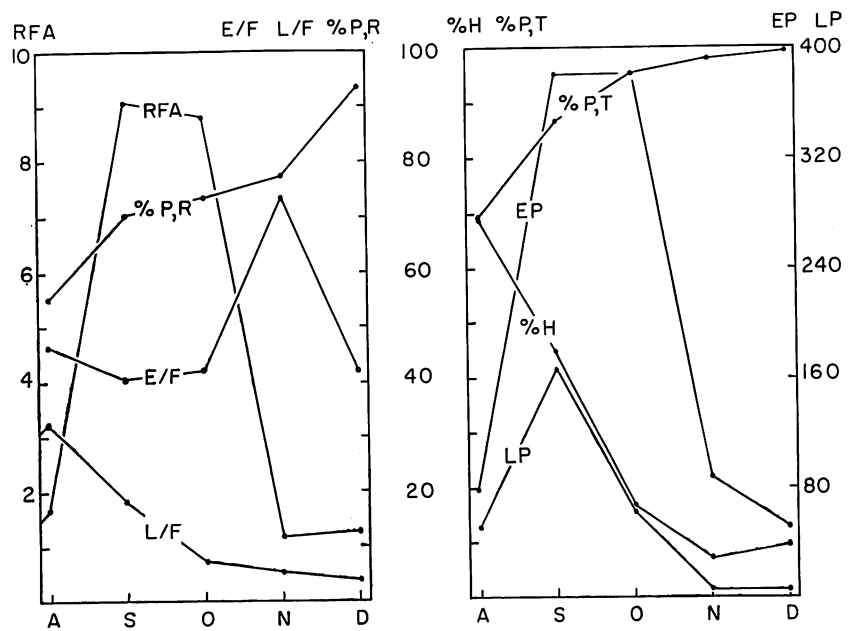

FIG. 7. *Cycles of relative fruit abundance (RFA), eggs per fruit (E/F), larvae per fruit (L/F), true % of parasitization (% P, T), % of parasitization by rearing (% P, R), hatch of eggs (% H), relative egg populations (EP), and relative larval populations. (LP). Based on a study of the fall fruit crop on windward Oahu, 1953. The area covered extended from Punaluu to Nuuanu.*

and infestation cycles were made as to leave no doubt of the critical relationship between the initiation of the fruiting cycle and greatly increased activity of flies. With the exception of 1951, maximum infestation in ground fruits followed the minimum in fruit abundance by just 1 month; in 1951, the rather weakly defined peak of infestation coincided with the fruiting minimum.

Ovipositional activity showed several notable features over the 5-month period. The number of eggs/fruit was relatively constant throughout the period, ranging between 41 and 47 eggs/fruit except for the month of November when it rose to 74 eggs/fruit. This appears to have been due to more intensive attack upon the fruit remaining after the drop from RFA 8.8 in October to RFA 1.2 in November. It should be noted, however, that while fruits were only 1/7th as abundant in November as in October, the corresponding increase in number of eggs/fruit was not 700% (as would be expected on a basis of strict proportionality) but only about 75%. This would indicate a reduction of about 90% in the relative ovipositional activity of the flies in November, while the actual decline in volume of males caught per day in the 4 methyl eugenol traps in this area was from 207 to 142 cc per day, or only about 30%. The remaining 60% of the decline probably stems from 2 sources: (1) the proportion of immature flies in the population in November was probably higher due to heavy mortality of spent females and (2) a factor which we must, in ignorance of its real nature, call a "behavioral" factor—the flies which were left simply appeared to lose interest in the fruits that were available, and spent their time in activities other than oviposition. Another case of this kind was described previously in the section on adult populations. Such an effect has been observed in too many cases to leave any doubt as to its reality—wild populations of *Dacus dorsalis* do not, to any great extent, compensate for decreases in fruit abundance by a proportional increase in concentration upon the few fruits remaining, but curtail their egg-laying activity instead. In this way they differ markedly from laboratory populations whose continuous breeding pattern is so well known.

By multiplying values for fruit abundance and number of eggs/fruit, a useful measure of the relative egg population is obtained. In August the relative egg population was 79.4; in September and October it rose sharply to just over 370; and it fell to 88.2 and 54.2 in November and December. Thus nearly 80% of the eggs laid during this 5-month cycle were laid in 2 months, and these 2 months also yielded 80% of the fruit.

Turning next to larval infestation, we find that the number of larvae/fruit is maximal in September, coinciding with the 1st upward swing in fruit abundance. While no records of tree fruits were taken in July the figures for ground fruit infestation showed that these were not as heavily infested in that month (23.9 larvae/fruit) as in August (30.2 larvae/fruit) so that it is quite safe to assume that the August infestation was maximal

for this cycle. After the high point of 32.1 larvae/tree fruit, the infestation fell steadily to 4.1/fruit in December. Infestation figures for ground fruits for the years 1950 to 1953 inclusive (Table 3) are in perfect agreement with this picture. In every year the story was the same; maximum infestation followed minimum fruit abundance by just 1 month.

Larval population is another matter, however, and here we find that the maximum larval population in tree fruits did not coincide with maximum infestation, but followed it by 1 month. In fact, 56% of the larvae produced in this particular 5-month cycle developed in the month of September. And again, we find essentially the same situation in the general ground fruit collections for 1950 to 1953, i.e., in each year except 1951, the maximum larval population was reached the month following the maximum infestation and 2 months after the minimum of fruit abundance.

Two facts should stand out among those that have been presented in the preceding paragraphs: (1) the number of eggs per fruit remained relatively uniform throughout the months of August to December 1953 varying from 40.9 to 73.5 and (2) at the same time the number of larvae per fruit fell steadily from 32.1 to 4.1. This clearly demonstrates the effect of egg mortality upon infestation levels. Under normal circumstances egg mortality is just as important as initial egg number in determining the final number of larvae/fruit. Where populations over large areas are concerned, the great seasonal variations in infestation which are such a familiar part of fruit fly biology, are governed primarily by egg mortality and not by differences in ovipositional activity on the part of the fly.

The role of microorganisms in egg mortality: The presence of bacteria and fungi in the dead eggs of *Dacus dorsalis* naturally leads to the question of whether the eggs were killed by these microorganisms, or simply by trauma associated with oviposition by *Opius oophilus*. As pointed out earlier in this section, these are probably the only factors which play any significant part in egg mortality, and it is virtually impossible to differentiate their effects under field conditions. There are, however, certain lines of evidence which are strongly indicative that both are involved and that egg mortality is not due solely to the cumulative physical effect of repeated parasite attacks.

The habit of *Dacus dorsalis* of revisiting old egg punctures to oviposit is paralleled by the parasite *Opius oophilus* which also may pay repeated visits to these old lesions. All observations by the writers point to the fact that this parasite is quite selective in its choice of eggs for oviposition. In experimental work with *O. oophilus* it is a common experience to find nearly all of a small lot of fruit fly eggs parasitized, but with only 1 or 2 containing 2 parasite eggs or larvae. This indicates that the parasites ordinarily do not superparasitize eggs as long as there is a ready supply of unparasitized ones. However, it is also true that under field conditions, where there is a large parasite population at work, many dead host eggs

will contain 2 or even 3, and rarely 4 parasite eggs or larvae.

In probing old lesions and eggs, the ovipositors of the parasites become contaminated with bacteria and fungus spores and these are then transmitted to intact eggs. This has been demonstrated by culturing these microorganisms from detached ovipositors, and also by making nutrient agar smears of eggs which had been exposed to parasites in the field then incubated for 24 hours. Such eggs, when smeared on agar slants, usually produced colonies of bacteria or fungi, or both. Moreover, when fresh eggs are laid among eggs heavily infected with bacteria and sporulating fungi, there is an immediate source of infection which can be transferred directly to the new eggs by the first parasite to revisit the lesion.

Several kinds of microorganisms have been cultured from infected eggs. These have been identified as *Penicillium* sp., *Serratia* sp. and a number of gram negative bacilli and cocci by E. A. Steinhaus and C. G. Thompson[6] of the University of California. Penicillium is the one which is most evident in old lesions, for it is the spores of this fungus which give these lesions their characteristic blue or black color. However, the bacteria are probably more directly involved in egg mortality than the fungi. All of these organisms would be considered nonpathogenic under normal conditions, but when they are inserted directly into the egg in large numbers, it is most probable that they are capable of causing pathological effects and even death.

One line of evidence for the existence of a mortality factor other than trauma lies in the great variation in hatch of eggs exposed to the same degree of parasite attack. In Table 9, the 3 minimum and 3 maximum

TABLE 9. *Comparison of minimal and maximal hatch of eggs exposed to the same degree of true % parasitization. The columns should be read vertically. The values in the last line show the approximate ratio of hatch of parasitized eggs in the minimal and maximal groups, calculated by the following formula:*

$$r = \frac{\%\ Hatch\ in\ Maximal\ Group - \%\ Unparasitized}{\%\ Hatch\ in\ Minimal\ Group - \%\ Unparasitized}$$

Range, true % P	100	99.0—99.9	98.0—98.9	97.0—97.9	95.0—96.9	93.0—94.9	90.0—92.9	84.5—89.9
Minimal Hatch	0.0	1.7	3.4	4.7	7.8	7.9	8.6	15.4
(3 samples)	0.0	1.8	3.4	6.0	7.9	9.5	9.6	16.7
	0.0	1.8	4.8	7.5	8.3	9.7	13.4	18.1
Av.	0.0	1.8	3.9	6.1	8.0	9.0	10.5	16.8
Maximal Hatch	36.2	16.5	21.4	36.6	37.8	66.9	60.6	54.7
(3 samples)	57.1	22.8	34.1	44.1	38.7	66.9	63.5	57.4
	68.6	23.4	40.5	90.0	49.4	89.3	72.4	81.2
Av.	54.0	21.1	32.0	56.9	42.0	74.4	65.5	64.4
r =	∞	15.8	12.0	15.0	9.5	22.8	28.5	12.9

[6]Now with the U. S. Department of Agriculture

values for egg hatch have been selected from 9 groups of samples. The members of each group have in common that they experienced very nearly the same degree of parasite attack as measured by the true % parasitism. It seems reasonable to assume that the parasites must have done just about the same relative amount of searching, probing and superparasitizing of those eggs which showed maximal hatch as those which showed minimal hatch, but the hatch varied greatly. Take, for example, the group of samples in which 97.0 to 97.9% of the eggs were parasitized. The 3 samples with minimal hatch averaged only 6.1% hatch, while the 3 maximal averaged 56.9% and reached 90.0% hatch. In each case, about 2.5% of the eggs were unparasitized and did hatch. In the minimal group, an additional 3.6% were parasitized and hatched, to give a total hatch of 6.1%, but in the maximal group, an additional 54.4% of the eggs hatched and these, of course, came from the parasitized eggs. Thus, 3.6/97.5 and 54.4/97.5 respectively, of the parasitized eggs in these 2 groups hatched, to give a discrepancy of 15 times in the degree of hatch in the minimal and maximal groups. While the relative effort (hence trauma) exerted by the parasites in parasitizing these 2 groups of eggs might have differed by a factor or 2 or possibly 3 times, it is certain that it did not differ by a factor of 15 times. The logical conclusion appears to be that something in addition to purely mechanical trauma is operating here and death due to infection is the only likely possibility.

If the foregoing is true, eggs which develop under conditions of reduced likelihood of infection should show relatively high rates of hatch at any given true % parasitization. In an expanding egg population, we have a situation which should lead to just such conditions—an increasing number of eggs, and a decreasing rate of revisitation of old stings. In a small and contracting egg population, the reverse should be true. It is therefore of interest to see if there are any seasonal trends in egg mortality which might substantiate the hypothesis that has been developed above. In Table 10, the data from the egg mortality studies were arranged according to month,

TABLE 10. *Comparison of observed and expected rates of mortality and parasitization by rearing (% P, R), Oahu, 1951-1952, to show seasonal trends. (Values for December based on only 3 samples)*

	J	*F*	*M*	*A*	*M*	*J*	*J*	*A*	*S*	*O*	*N*	*D*
True % Par.	96.8	88.6	83.7	95.5	97.7	95.8	95.6	94.1	94.3	96.3	96.9	87.8
Expected Mort.	86.1	64.5	56.1	82.0	88.0	83.2	82.8	78.0	78.6	84.7	86.7	63.0
Observed Mort.	92.8	72.9	45.8	82.0	90.8	81.0	83.2	69.2	81.9	84.6	90.8	85.6
Expected % P, R	77.7	67.9	63.5	75.7	79.7	76.2	76.0	73.9	74.1	77.0	77.9	67.0
Observed % P, R	54.8	58.0	69.9	74.7	74.9	77.9	73.8	80.8	68.7	75.7	66.4	43.7
Mort. $\frac{\text{Observed}}{\text{Expected}}$	108	113	82	100	103	97	101	89	104	100	105	140
% P, R $\frac{\text{Observed}}{\text{Expected}}$	71	85	110	99	94	102	97	109	93	98	85	65

and the true % of parasitization and mortality for each month were determined. These values were then compared with the expected values read from the curves in Fig. 6. A study of the table will show that exceptionally low mortalities were observed in March and August, and it is at just these times that egg populations are beginning to increase. Exceptionally high values were noted in December, January and February, when fruit abundance and egg populations are at their lowest point and all stings are heavily infected with mircoorganisms.

When observed mortality rates are markedly lower than the expected rates, this means that more parasitized eggs are surviving than would be normal for that particular true % of parasitization. Consequently, observed rates of parasitization by rearing are higher than normal. The reverse is true when survival of parasitized eggs is lower than normal. At such times more parasitized eggs are dying, relatively fewer parasites are emerging and rates of parasitization by rearing are relatively lowered. This is precisely what is seen in Table 10 and it is felt that the seasonal discrepancies between observed and expected values for % parasitization by rearing have their basis in differential mortality of parasitized eggs, stemming from differences in numbers of eggs dying of infection.

In conclusion we can state that egg mortality is one of the most important natural control factors in the life of both *Dacus dorsalis* and *Opius oophilus*. This alone, on a % basis, accounts for more host individuals than any other factor, and numerically it accounts for more than 5 times as many developing *D. dorsalis* as all other factors combined. While it is quite certain that both trauma and infection are involved in killing eggs, it is not possible to state which is more important. The relative importance of the 2 factors undoubtedly fluctuates seasonally.

LARVAL AND PUPAL MORTALITY

Upon hatching from the egg, the larva encounters another group of hazards, including toxic substances produced by saprophytic fungi and bacteria, drowning, larval parasites, predators, pupal parasites, extreme heat and competition from other larvae. These factors exert their influence from the time the larvae hatch from the egg until the flies emerge from the puparia and in some cases even beyond that. Because of the variety of these and the close interdependence of some of them, it is not feasible to study each separately. However, they can be analyzed collectively by exposing infested fruits in the field, simulating natural conditions as closely as possible.

Combined larval and pupal mortality: Two methods of exposure were tried in studies on larval and pupal mortality. The early exposures were made in frames 18 in × 18 in × 4 in (inside dimensions), in which 18 to 20 fruits were placed. In later studies, smaller frames (6 in square) were employed, each frame holding only 2 fruits. These made possible the dis-

tribution of the fruits comprising a sample over a wider range of conditions at any given site and it was thought that this would give results somewhat more typical of the site as a whole than would the larger frames. Actually, the results obtained with the 2 types of frames were so nearly alike that it would be difficult to say that one was better than the other although in principle, the small frames appear preferable. Both types of frames, with accessories, are shown in Figs. 8 and 9.

In the early studies, relatively intact guava fruits were picked from the ground in matched pairs; 1 fruit of each pair was placed in 1 container, and 1 in another. This was repeated until 18 to 20 pairs of fruits had been collected and divided into 2 samples. One sample was held as a check, the fruits being dissected and held for recovery of all larvae, while the other sample was placed in a frame in the field. Altogether, 32 lots of fruit were exposed in frames and 32 held as checks, a total of more than 1200 fruits.

After the fruits had been set in the frames, the frames were covered by a piece of 3/4 in mesh hardware cloth to keep out rodents and birds. At the end of a week, this was removed and 4 glass plates, 3 in by 17 in, coated with "Tanglefoot", were set on wire supports in the frames to catch emerging flies and parasites. It was necessary to mix benzoic acid with the

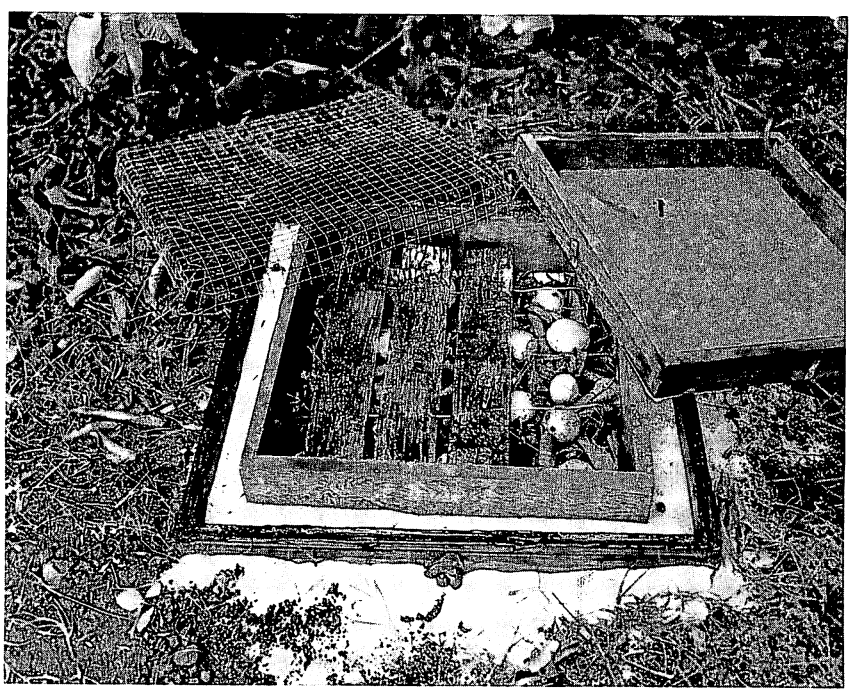

FIG. 8. *Large frames used in early studies of larval and pupal mortality, showing rat-guard, "tanglefoot" and sand ant barriers, and the sticky plates used to trap emerging flies and parasites.*

FIG. 9. *Small frames used in later studies of larval and pupal mortality. The fruits were covered with the coarse mesh cage for the first few days, then this was replaced by the fine mesh frame, of which both inside and outside views are shown. The wire tower and glass jar are shown being put on the frame.*

"Tanglefoot" to prevent growth of molds which interfered with the identification of the forms captured. The whole frame was then covered with a tight screen lid and lined with organdie, to prevent escape of the parasites. The frames were examined once a week until it was evident that emergence was complete. The plates were then removed to the laboratory where the flies and parasites were counted.

The check fruits were dissected and examined daily until it was certain that all larvae had been removed. These larvae were transferred to blended papaya medium and reared to maturity to determine incidence of parasitism.

Certain changes were made in the later studies. Yellow-ripe tree fruits were used instead of ground fruits, and these were tossed to a height of about 10 feet, falling to the ground through the branches of a guava tree. Check samples were not treated in this manner, however. Thus, mortality throughout the entire period on the ground was measured, while in the earlier studies the mortality incurred during the 1st day or 2 the fruits were on the ground was not measured. In reality, this would not affect the conclusions reached unless the mortality during the 1st day on the ground was

disproportionately high, which did not appear to be the case. The guavas were then placed, in pairs, under a small cage made of hardware cloth with a wooden cleat on each end (Fig. 9). The cage was held to the ground by a large spike at each end, passing through a hole in the cleat. For 3 or 4 days the fruits were completely exposed, for all practical purposes, except that birds and rodents were excluded. At the end of this time, they were covered with the 6 in × 6 in brass screen frames. These had a pyramidal top of 1/32 in mesh screen. The pyramid was cut off to a square top, and to this was soldered the metal lid of a 4-ounce wide-mouth jar.

A square hole was previously chiseled out of the lid and a collar of galvanized metal soldered into this hole. This left a trough around the square opening and in this trough was placed a viscous preservative made up of 500 g mineral oil, 200 g vaseline, and 5 g benzoic acid. Because flies were sometimes able to crawl over the galvanized metal collar and back down into the frame after falling in the preservative, it was necessary to fit a small tower of stainless steel screen over the collar. This was closed with screen at the upper end but 4 small holes punched in the sides of the tower allowed the flies and parasites to pass into the jar. An indication of the effectiveness of this arrangement in recovering specimens is the fact that most adults of *Dacus* and *Opius* captured were very teneral, showing that they were only a few minutes old at the time they fell into the preservative.

The base of the frame was made of 4 strips of fir. In each of these a sloping hole was bored to permit entrance of ants and a screen baffle in front of the inner end of each hole minimized the chance of escape of larvae, flies, or parasites. A projecting strip of heavy sheet metal was nailed around the inside of the base and this was forced into the soil to prevent larvae from crawling into or out of the frame. A special cutter of sheet steel mounted on a heavy wooden base was used to break the soil so that the frames could be installed without damage. A rubber collar around the jar, projecting over the inverted cap, kept rain from displacing the preservative in the cap. The fruits were covered with these frames until it was certain that emergence was complete. Final counts of the flies and parasites were made, predator activity observed, and the frames removed.

The 1950 experiments were carried out in 2 areas on Windward Oahu. The lower Waimanalo site, as it will be designated, lay at an elevation of about 150 ft, 0.8 miles northeast of the summit of Olomana Peak, while the Pali Road area lay at an elevation of about 500 ft, 2.0 miles northwest of the summit of Olomana Peak. The lower Waimanalo area was considerably drier and somewhat warmer than the other, although rainfall in the 2 was probably about the same. Guava, lantana, and koa haole growing in red clay soil characterized the drier site, while the Pali Road site was characterized by guava, mango, and kukui nut growing in a black soil rich in humus. The differences were due more to lowered evaporation rate in the upper area than to heavier precipitation. This area was cover-

ed more by clouds and lay close to the steep-walled Koolau range, which protected the site from the wind and late afternoon sun.

The 1st frames were installed in June and August 1950, 16 frames in all being used. Four of these were intended to provide a check on the effect of excluding predators, but failure of the barriers permitted reinvasion by ants. Four others were lost when some of the fruits were removed by scavengers. Considering those experiments in which parasites and predators had relatively unlimited access to larvae or pupae, the ratio of total flies and parasites caught on plates in the field to the initial larval infestation was as given in Table 11. These figures show that 11 to 63% of all larvae in these samples at the time of collection eventually pupated and produced either flies or parasites. The checks held in the laboratory produced a total of 783 larvae, while only 184 flies and parasites were captured in the frames, indicating a survival in the field of 23.5%. The mean survival in 8 samples was 27.2%. Therefore, it would appear that about 75% died either as larvae or pupae.

TABLE 11. *Data on survival in exposed fruits in lower Waimanalo and Pali Road areas, Oahu, June to August, 1950. Frames to which predators had virtually unlimited access*

Locality	*Frame No.*	*Larvae (checks)*	*Emerged in frames*			*Total emerged larvae in checks (survival)*
			Dacus	*Opius*	*Total*	
Lower Waimanalo	1	113	3	9	12	10.6%
	3	140	8	15	23	16.4%
	11	74	8	6	14	18.9%
	14	115	12	25	37	32.2%
		442	31	55	86	19.5% ; 19.5%
Pali Road	5	131	12	11	23	17.5%
	7	92	3	18	21	22.8%
	9	43	4	23	27	62.8%
	15	75	7	20	27	36.0%
		341	26	72	98	28.7% ; 34.8%*
Both Sites		783	57	127	184	23.5% ; 27.2%

*28.7% based on total emerged survival/total larvae: 34.8% based on average of the four values.

The rather large error inherent in this type of study makes it difficult to assess the significance of the difference between the 2 sites. However, in a 2nd series of experiments ran in the same sites a short time later, survival in the Pali Road area was again higher than in the lower Waimanalo site. This 2nd series of frames was run from August to October 1950 using essentially the same procedures as before, except for an improved ant barrier. Considering those experiments in which parasites and predators had relatively unlimited access to larvae and pupae, the ratio of total flies and para-

TABLE 12. *Data on survival in exposed fruits in lower Waimanalo and Pali Road areas, Oahu, August to October,* 1950. *Frames to which predators had virtually unlimited access*

Locality	*Frame No.*	*Larvae (checks)*	*Emerged in frames* Dacus	Opius	*Total*	*Total emerged larvae in checks*
Lower Waimanalo	1A	99	1	0	1	1.0%
	3A	82	1	2	3	3.7%
	11A	78	6	7	13	16.7%
	14A	70	7	15	22	31.4%
		329	15	24	39	11.9% ; 13.2%*
Pali Road	5A	87	6	17	23	26.4%
	7A	85	3	18	21	24.7%
	9A	36	5	11	16	44.4%
	15A	59	4	6	10	16.9%
		267	18	52	70	26.2% ; 28.1%
Both Sites		596	33	76	109	18.3% ; 20.7%

*11.9% based on total emerged/total larvae; 13.2% based on average of the four values.

sites caught on the "Tanglefoot" plates to larval infestation in the checks was as given in Table 12. Here it can be seen that the survival in both areas was lower than in the 1st run, which may have been due to fruit condition, increased predation rates, or some other factor. The weather was noticeably warmer and drier during this 2nd run, but there is no certainty that this was more than indirectly responsible for the observed difference.

The 1951 and 1952 studies were carried out in the small frames described above, and also with the use of tree fruits rather than ground fruits. The experiments were conducted at 2 sites on Windward Oahu, 1 characterized as dry, the other as very wet. The dry or Kailua site lay at an elevation of about 75 ft, 1.7 miles northwest of the summit of Olomana Peak, while the wet or upper Waimanalo site lay at an elevation of 150 ft, 1.6 miles southeast of the summit of Olomana Peak. Rainfall was about the same in both areas. From 22 October 1951 until 21 October 1952, 51.2 in of rain fell in the Kailua area and 55.1 in in the upper Waimanalo area. Yet the ground cover was almost tinder-dry much of the time in the Kailua area and almost constantly wet in the Waimanalo area. This difference was attributable, as in the case of the lower Waimanalo and Pali Road areas, to differences in cloud cover and shielding from the wind and afternoon sun by the Koolau Range. The vegetational differences between the 2 sites were similar to, but somewhat more marked than, those which existed between the Pali Road and lower Waimanalo sites. The data from the 3 sets of experiments ran in these areas are very briefly summarized in Table 13.

Relative abundance of ants was measured by counting the number of

TABLE 13. *Summary of studies with 6 in × 6 in exposure frames, windward Oahu, October, 1951-June, 1952. Each experimental sample contained 20 fruits in 10 frames. Each laboratory control consisted of 10 fruits. Total ants = total counted in ten 6 in × 6 in squares. Larvae/20 fruits obtained by doubling the number from the 10 check fruits. Frames removed and earwigs counted at time of last ant count*

Date set out	*Ants counted*		*No. earwigs*	*No. Dacus*	*No. Opius*	*Total Surv.*	*La./20 fruits*	*% Mort.*	*% Surv.*
	Date	*No.*							
Upper	*Waimanalo*								
Oct. 22	Oct. 26	15							
	Nov. 26	9	11	2	0	2	14	85.7	14.3
Feb. 11	Feb. 14	2							
	Feb. 26	9							
	Mar. 18	3	2	4	70	74	672	89.0	11.0
Apr. 23	Apr. 25	8							
	May 6	5							
	June 10	38	20	82	26	108	778	86.1	13.9
		1.1/frame						86.9	13.1
Kailua									
Oct. 22	Oct. 26	148							
	Nov. 26	56	0	1	7	8	28	7.14	28.6
Feb. 11	Feb. 14	50							
	Feb. 26	191							
	Mar. 18	53	0	56	103	159	672	76.3	23.7
Apr. 23	Apr. 25	55							
	May 6	78							
	June 10	41	0	103	70	173	778	77.8	22.2
		8.4/frame						75.2	24.8

ants within a 6 in × 6 in frame placed on the ground at 10 points within the experimental area. The points were selected arbitrarily with respect to the frames, usually 1/2-way between frames. Because earwigs have been shown to be predaceous upon *Dacus* larvae in guava fruits, a check was also made on these at the time the frames were removed.

The largest number of earwigs counted was 20 in 20 fruits at the upper Waimanalo area, 10 June 1952. While it might be tempting to attribute the higher mortality of *Dacus* larvae and pupae here to the presence of earwigs, other factors were probably of greater importance. The lower temperature and constant wetness of the ground led to a more rapid decay of the fruits in the upper Waimanalo frames, conditions known to have a detrimental effect on larval survival. These factors alone could easily produce a difference of the magnitude observed, hence it is unlikely that the earwigs accounted for any more than an insignificant part of the mortality. It is apparent that the differences in mortality during the 3 runs were so small as to be insignificant in this type of experiment, while variations in the earwig counts were appreciable.

Another fact that is apparent from these data is that the absence of effective predators at the wetter site was more than offset by mortality from other sources. Considering the data in terms of survival, almost twice as many flies and parasites were produced in the Kailua frames, despite the presence of about 8 times as many ants. Again, this difference is probably due to the unfavorable influence of decay organisms in the cooler, wetter site.

It is also important to note that the mortality was not influenced by the larval density to any significant extent. The infestation in the 2nd and 3rd runs was 25 to 50 times as great as in the first, while the mortality was only about 16% lower. There is no way of estimating the significance of this small difference with the limited data available.

Mortality attributable to soil fauna: During the 2nd series of experiments in 1950, one group of 18 in × 18 in frames was set aside for study of the effect of the elimination of the soil fauna. Prior to placing the fruits, 2 barriers of coarse sand and a 3rd barrier of tanglefoot were placed around each frame to exclude ants. A small amount of carbon tetrachloride was then introduced and the frame was covered for about an hour to kill all insects inside the frame. Treated and untreated frames were paired in order to determine the mortality attributable to predators. While variation between frames was greater than desirable, the writers feel that the results obtained by combining experiments in which the frames had a similar history of treatment are not misleading. The data are presented in Table 14.

Unfortunately, 3 of the treated frames were reinvaded by ants and this must be considered in making the analysis. The remaining 5 frames produced a total of 116 flies and parasites, compared with 433 larvae in the controls, indicating a survival of 26.8% of the larvae originally in the fruit. Only 52 flies and parasites were produced in the untreated frames, compared

TABLE 14. *Comparison of total emergence (T) of flies and parasites with number of larvae in checks (L), treated and untreated frames. Significant reinvasion by ants occurred in frames 2A, 11A, and 54 (marked with asterisks). W=lower Waimanalo; P=Pali Road*

				Not defaunated				
Locality	*W*	*W*	*W*	*W*	*P*	*P*	*P*	*P*
Frame No.	*3A*	*1A*	*12A*	*13A*	*4A*	*7A*	*9A*	*15A*
T/L (%)	3.7	1.0	14.9	10.5	26.7	24.7	44.4	16.9
T	3	1	7	4	12	21	16	10
L	82	99	47	38	45	85	36	59
				Defaunated				
Frame No.	*2A**	*6A*	*11A**	*14A*	*5A**	*8A*	*10A*	*16A*
T/L (%)	13.1	11.1	16.7	31.4	26.4	39.0	17.6	30.9
T	13	9	13	22	23	48	16	21
L	99	81	78	70	87	123	91	68

with 317 larvae in the controls, for a net survival of only 16.4%.

Using these values, the emergence in the 5 treated frames was: $100\left(\frac{26.8-16.4}{16.4}\right)=63.4\%$ higher than in the untreated frames.

If the 2 areas are considered separately, there was an appreciable difference in the effect of the soil fauna. Adding values for T and L from each locality and calculating the survival (100 T/L), the following figures for increase in survival are obtained:

Lower Waimanalo	Pali Road
$100\left(\frac{17.4-5.6}{5.6}\right)=210.7\%$ increase	$100\left(\frac{29.3-26.2}{26.2}\right)=11.8\%$ increase

On the basis of these figures, there was only a slight increase in emergence attributable to the elimination of the soil fauna at the Pali Road site, while at the lower station the emergence was approximately doubled. Both values were undoubtedly lowered by the reinvasion of certain of the frames by ants. Nevertheless, the difference strongly suggests a greater activity on the part of predators in the lower, drier, warmer site. Such a difference in the activity of ants (especially *Pheidole megacephala*) was actually observed throughout the course of the study. Although present in both areas, ants were much more numerous and aggressive in the lower Waimanalo frames.

Considering the available data in terms of mortality, it is obvious that the majority of the mortality in the larval and pupal stages is caused by factors other than predators. In the 8 treated frames, 76.3% of the total larvae failed to produce flies or parasites, compared with 84.9% in the untreated ones. If the remaining 8.6% is attributed solely to predators, then predators accounted for only 8.6/84.9 of the total larval or pupal mortality (10.1%). Considering the Waimanalo area alone, 82.3% of the larvae in the treated frames died, while in the untreated ones, 94.4% failed to mature. The difference of 12.1% amounts to 12.1/94.4 or 12.8% of the total mortality caused by all factors operating on the larvae and pupae. If the values for survival arrived at above are too low, due to reinvasion of the frames, then by the same token the figure of 12.8% mortality of larvae and pupae is also somewhat lower than can be attributed to predators acting alone; 15% would be a closer estimate for the Waimanalo area.

The importance of any particular mortality factor, of course, is determined by the mortality induced in that segment of the survival population upon which it operates. In the present case, only 23.7% of the larvae produced flies, even in the absence of predators, while when predators were admitted, this value was further reduced to 15.1%. Mortality induced by predators in that segment of the population exposed to predation in the present experiments was, therefore, $100\left(\frac{23.7-15.1,}{23.7}\right)$ or 36.3%. Again, the reinvasion of some of the frames resulted in a survival population which

was lower than it would have been without reinvasion, so that the value of 36.3% predator-inflicted mortality is lower than it should have been; 40 to 45% would be the maximum estimate that could be made reasonably, however.

Pupal mortality: The field experiments described above showed that the majority of larvae which hatch from the eggs die before they mature and, that the majority of these are killed by factors other than predators. In order to determine more precisely what these factors are, laboratory tests were designed to show whether they were operating in the soil, in the fruit, or both. Outside of predators, the principal factors which might influence mortality in the soil appeared to be microorganisms, excessive moisture or dryness, and extremes of temperature. Only the 1st 2 of these were studied.

About 12 pounds of soil, rich in humus, were collected from a guava thicket on Mt. Tantalus, passed through a 3/32 in sieve and air-dried in the shade. This soil was run through a sample splitter repeatedly until 20 wide-mouth jars had been 1/2-filled with soil. The weight of the air-dried soil was then adjusted to 200 g. Ten of the jars were baked in an oven at 140 C for 1-1/2 hours. During this time they were covered, except for 2 which were left open to determine the amount of hygroscopic water. These 2 lost 17.5 and 18.0 g (8.9% hygroscopic water).

After baking, each jar was weighed again. Water was then added to the unsterilized jars to make up a series approximating 10, 15, 20, 25, 30, and 35% moisture, the actual values being given in Table 15. The same was done for the sterilized series, except that an additional ml of water was added for each gram of weight lost. One jar (*S–O*) in which the moisture content was nearly zero was set aside. The last member in each series contained water slightly in excess of the holding capacity of the soil (36.5%, by weight), so that the soil at the bottom of the jar was perceptibly wetter than near the top.

Sixty larvae, sterilized in 95% alcohol, were placed in each jar. These were from a uniform and vigorous stock reared by Glenn Finney of the University of California. The jars were stored at laboratory temperature until emergence was complete. They were kept loosely covered throughout the study, and were aerated daily. Data recorded were: number of larvae pupated and number of adults emerged. In Table 15 these have been expressed as %.

A study of Table 15 will show that no mortality whatever could be attributed to soil microorganisms. Pupation and emergence were essentially the same in the 2 series and the survival (95.2%) was identical.

The results obtained in *S*–0, *S*–1, and *U*–1 show that no significant mortality was encountered in soils until they are dried by removal of hygroscopic water. In the present case, all of the mortality due to insufficient moisture lay in the narrow range between 0 and 9% water content.

TABLE 15. *Summary of data on survival of* Dacus dorsalis *larvae in sterilized and unsterilized soils. Percent water by weight is given as an average of initial and final percentages, and includes hygroscopic moisture. % survival = 100 × flies emerged/60*

Jar	% *water*	% *larvae pupated*	% *puparia producing flies*	% *survival*
Unsterilized (U)				
U—1	8.8	96.7	89.7	86.7
U—2	12.8	100.0	98.3	98.3
U—3	17.9	100.0	96.7	96.7
U—4	22.1	98.3	100.0	98.3
U—5	26.9	100.0	93.3	93.3
U—6	31.6	100.0	100.0	100.0
U—7	36.0	98.3	94.9	93.3
Averages		99.0	96.2	95.2
Sterilized (S)				
S—0	2.3	15.0	0.0	0.0
S—1	8.6	100.0	96.7	96.7
S—2	13.5	100.0	98.3	98.3
S—3	18.0	98.3	98.3	96.7
S—4	22.2	98.3	100.0	98.3
S—5	26.9	98.3	94.9	93.3
S—6	31.5	98.3	98.3	96.7
S—7	36.1	95.0	91.2	86.7
Averages (S-O omitted)		98.3	96.9	95.2

Soils in which the water content is below the level of equilibrium with atmospheric moisture apparently act as a dehydrating medium. It is probable that soils differing in their hygroscopicity also differ in the level at which a declining scale of moisture content will begin to cause mortality by dehydration. However, this is not universally true, for the mortality of pupae in sand (which is very weakly hygroscopic at the most) is sometimes high when the relative humidity of the air is low. Here, mortality is brought about by loss of water to the interstitial air alone, and there is no loss of water from the air to the surrounding sand.

Dehydration of pupae in the soil is probably not a very important mortality factor, except in extremely dry and hot situations which are unfavorable to most hosts. Direct and prolonged exposure to the sun would be required to keep the moisture below the level required for pupal survival, and under these conditions it would be difficult to distinguish between mortality due directly to heat, and that due to dehydration.

The experiment described above utilized air-dried soils in which the water content was adjusted to a particular level. Since this drying undoubtedly affected the activity of soil microorganisms, a 2nd experiment was designed utilizing undried soils. Soil samples were collected at 3 guava

sites: (a) Manoa Valley, Woodlawn —an extremely heavy, rich, black soil with a high humus content, (b) Pali Road —a lighter, more friable soil, but rich in humus, (c) Pali Road —an unusual coarse, sandy soil, low in humus.

The experiment was set up as before, using 200 g of soil and 60 larvae in each jar. The larvae were not sterilized, however. Four jars were used for each soil type, 2 of which were loosely covered with a metal cover, and 2 of which were covered with cloth. The latter lost from 16 to 20 times as much water as the former, but this had no effect whatever on the results (Table 16). Survival was not influenced in any way by the drying that took place. Survival in the Woodlawn samples was consistently lower than in the other samples, although the significance of this is not clear. Apparently the conditions in this soil were unfavorable for pupation. The emergence from pupated larvae was just as high as in the other samples, but the % of larvae forming puparia was appreciably lower. Survival in all 12 samples combined was 95.9%, compared with 95.2% in the 1st experiment. It must be concluded that there is no significant difference in survival of larvae in dried and non-dried soils. Furthermore, on the basis of these studies, it appears that there is no significant mortality of healthy larvae and pupae in the soil, outside of that inflicted by predators, or in exceptional cases, drowning, heat and dehydration.

TABLE 16. *Summary of data on survival of* Dacus dorsalis *larvae in unsterilized and undried soils*

Jar	% *water, by weight* Original	Final	% *larvae pupated*	% *puparia producing flies*	% *survival*
Pali Road (sandy)					
Closed a	21.5	20.5	96.7	100.0	96.7
b	21.5	20.5	100.0	100.0	100.0
Open a	21.5	4.5	100.0	100.0	100.0
b	21.5	5.2	100.0	98.3	98.3
	Averages		99.2	99.6	98.8
Pali Road (high humus)					
Closed a	25.8	25.0	100.0	98.3	98.3
b	25.8	25.0	100.0	100.0	100.0
Open a	25.8	8.5	100.0	100.0	100.0
b	25.8	8.5	100.0	100.0	100.0
	Averages		100.0	99.9	99.9
Woodlawn					
Closed a	42.6	41.3	85.0	100.0	85.0
b	42.6	41.8	91.7	100.0	91.7
Open a	42.6	18.8	88.3	98.3	86.7
b	42.6	20.1	93.3	100.0	93.3
	Averages		89.6	99.9	89.2

Natural mortality of pupae in the soil from causes other than natural enemies is much higher than one would anticipate from these experiments, even under favorable conditions. The writers believe that most of this represents mortality of pupae developing from weak larvae which would not have matured under the most favorable circumstances. The larvae used in these experiments were in excellent condition and survived better than would larvae reared from field fruits.

It is therefore concluded that the great majority of the mortality in larval and pupal stages actually occurs in the larval stage, or is the result of unfavorable conditions in the larval environment leading to the development of weak pupae.

Mucor and other decay fungi in fruit fly mortality: Since the studies discussed above all pointed toward the larval environment, exclusive of predators, as the direct or indirect source of most larval and pupal mortality, this environment was investigated to determine more closely the factors responsible. In the early studies on hatching of eggs, it was found that the mortality of larvae in fruits held in individual jars in the laboratory was extremely low—dead larvae were rarely found. But occasional guavas were found which contained a high proportion of dead or inactive larvae. In each of these cases it was noted that the fruit was undergoing a characteristic type of breakdown, with excessive gas formation and an acrid odor. Within a day these fruits would become covered by a dense, yellow, velvety mat of sporophores of 1 or more species of *Mucor* (Phycomycetes) commonly found attacking guavas on the ground. Subsequent observations established that this particular fungus is one of the most important factors in the bionomics of the fly.

Species of *Mucor* are normal components of the soil flora and attack a variety of vegetable products. The rapidity of growth of the fungus is one of its outstanding characteristics. Within 2 days of the time of infection, an entire guava can be converted into a veritable mycelial ball, and within 24 hours of the appearance of the 1st sporophores, the surface of the fruit can be covered by an unbroken mat of spore bodies. At the same time, the tissues of the fruit undergo a semi-liquefaction. This rapidity of fruit breakdown is probably as important as any factor in killing the developing larvae, although the byproducts of decomposition undoubtedly include a number of toxic compounds. Succinic, lactic, and oxalic acids, ethyl alcohol and ammonia have been reported among the metabolites of various species of *Mucor*.

Several experiments were conducted to get a measure of the relative importance of this fungus. The design of these experiments varied from 1 time to another, so that they are not strictly comparable; but they are consistent in showing that, when *Mucor* is present and abundant, the number of mature flies (or parasites) produced in guavas is materially reduced. There is not ample space to describe in detail how these tests were conduct-

ed, although this is available in the reports of the Hawaii Agricultural Experiment Station and of the Cooperative Fruit Fly Investigations (1951, 3rd and 4th quarters). In every case, the fruits were collected and distributed by rotation among the samples in such a way as to obtain a thorough randomization. The samples were kept in rearing jars (Fig. 10 and 11) and allowed to stand until all fruits had broken down and development of larvae was complete. The fruits were then opened to drive out any mature survivors which might otherwise be lost.

Three principal variables were introduced into these experiments; the fruits were: (1) either completely unsterilized or were disinfected externally by dipping in a copper salt solution, (2) either dropped on a firm surface or not dropped and (3) either inoculated with *Mucor* spores or not inoculated. In the case of the dropped samples, the fruits were allowed to fall about 7 feet into a tray of soil. If the fruits had been disinfected,

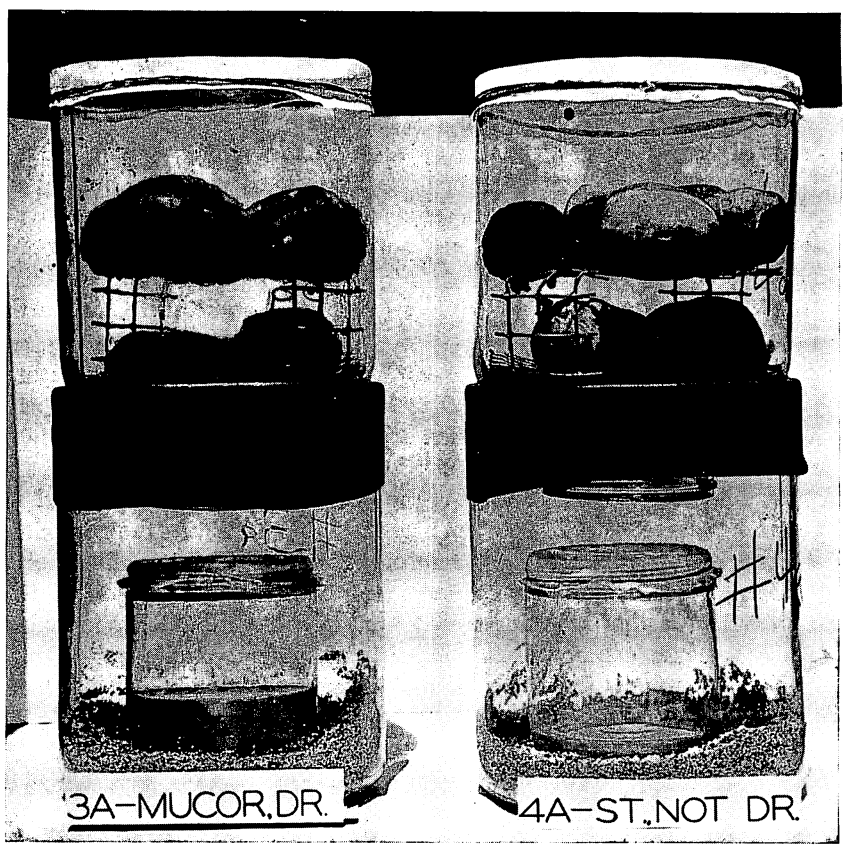

FIG. 10. *The tree fruits on the left were dipped in a suspension of* Mucor *spores and dropped, those on the right were dipped in copper acetate solution and not dropped. Note heavy growth of* Mucor *and large quantity of fluid in trap* (3A).

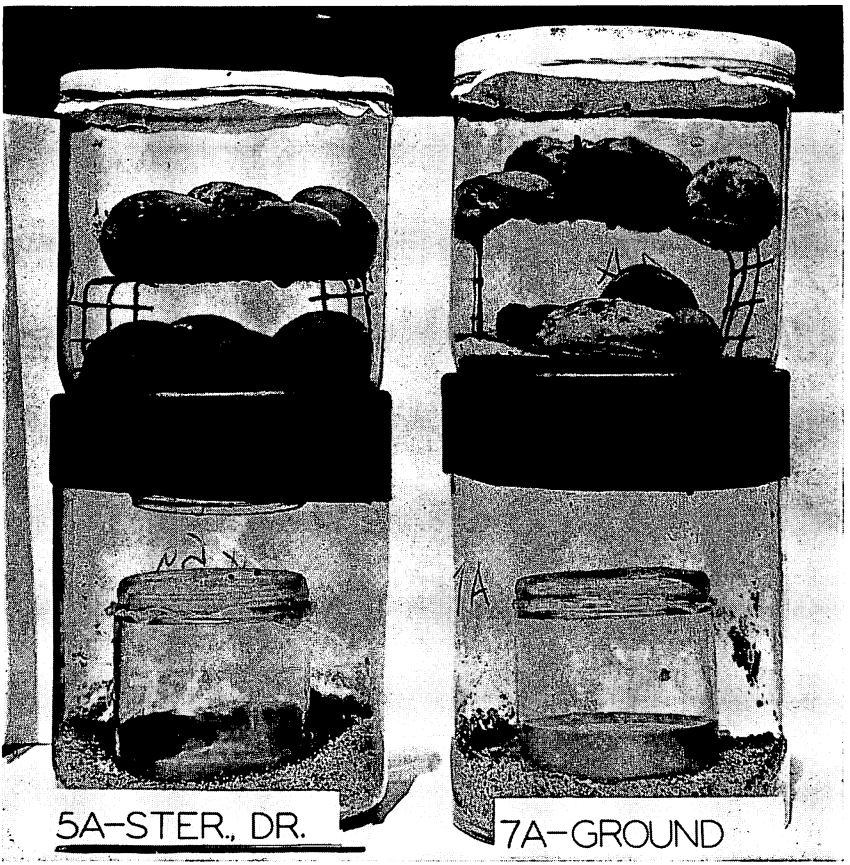

FIG. 11. *The tree fruits on the left were dipped in copper acetate, then dropped on a disinfected surface; those on the right were picked from the ground where they had become naturally infected with* Mucor *and other fungi. Compare samples* 3*A and* 7*A.*

the surface of the soil was covered with a sheet of copper- treated rubber or heavy paper to prevent reinfection and the holding jars were likewise disinfected. The dropping experiments were conducted simultaneously with the *Mucor* experiments because of the belief expressed by some investigators in the fruit fly investigations that the concussion sustained when the host fruits fell from the trees was a major factor causing mortality of larvae. The results of the present experiments and other observations do not support this belief, but do offer an alternative explanation.

Three separate experiments are summarized in Table 17. To simplify comparisons, the numbers of adult flies or parasites emerging from each lot of fruits are given both in actual figures and in %. In all cases, the maximum yields of adults were obtained from fruits dipped in fungicides and held without other treatment. Minimum yields were from those

TABLE 17. *Total emergence from samples of guavas treated in various manners. In the left 3 columns, the yields are given as total flies and parasites, while in the right columns the same fiigures are converted to percentages of the total yield for each experiment. A dash indicates that the particular treatment was not included in this experiment*

	Actual yields in experiment no.			*Percentage yields in experiment no.*		
Treatment	1	2	3	1	2	3
Sterilized, Not Dropped	335	68	549	32%	31%	33%
Not Sterilized, Dropped	312	39	427	30%	18%	25%
Sterilized, Dropped	154	45	382	15%	21%	23%
Not Sterilized, Not Dropped	—	27	—	—	13%	—
Ground Fruits	153	20	—	15%	9%	—
Mucor, Dropped	—	17	—	—	8%	—
Mucor, Not Dropped	81	—	322	8%	—	19%
(No. Fruits per Sample)	(20)	(19)	(40)	—	—	—
Totals	1035	216	1680	100%	100%	100%
Larvae dissected from untreated checks-		136	638			

fruits inoculated with *Mucor*. In the first 2 experiments, the *Mucor*-treated samples produced only 1/3 as many flies and parasites as the disinfected fruits. It should be noted that in the 3rd experiment the guavas were inoculated by piercing with fine wires. These fruits were unusually dry as a consequence of drought and only very limited *Mucor* infections developed.

It was pointed out above that the rate of breakdown, in conjunction with the semi-liquefaction of the fruit, is an important factor in the high mortality of larvae. The high rate of production of liquid is indicated in Fig. 10 which shows 2 lots of fruits from the 2nd *Mucor* experiment, about 6 days after treatment. The 9 fruits in jar 3A were dipped in a suspension of *Mucor* spores and also dropped, while those in 4A were dipped in fungicide and not dropped. The 1-pint trap in jar 3A contained approximately 135 ml of liquid, while there was not enough in 4A to cover the bottom (5 ml). Jar 5A (Fig. 11) produced only about 10 ml of liquid (the cloudy appearance in the trap was due to a heavy growth of mold). Jar 7A contained ground fruits which were collected the same time as the tree fruits making up the rest of the samples, and these fruits yielded 120 ml of liquid (its replicate, jar 7B, not shown here, produced 220 ml of fluid). The guavas in 3A and 7A are covered with a dense pile of *Mucor*, while 4A and 5A are mainly infected with fungi of other genera.

The effects of dropping were not clear cut. Although dropped samples sometimes produced flies or parasites at a lower rate than the ones which were not dropped, this was not always true. It is necessary to keep in mind that none of these fruits was actually sterilized, but only treated externally to eliminate *Mucor* and in general to reduce the rate of decay.

Most egg lesions contain innumerable bacteria and fungus spores, and these would not be affected to any extent by dipping in solutions of copper salts. The dropping would, however, soften the fruits appreciably and accelerate the rate of invasion by the microorganisms already within the fruits. A comparison of the amounts of liquid produced by the fruits in jars 3A and 5A is illuminating with respect to the effect of dropping on liquefaction. Both of these samples were dropped, hence the chief difference between them is in their microfloras. The microflora of sample 3 was dominated by *Mucor*, that of sample 5 by other fungi. Heavy infection by *Mucor* is always associated with copious production of liquid, except under drought conditions.

Mucor is abundant everywhere in guava-producing areas of the islands, and it is all but impossible for a fruit falling to the ground not to become inoculated with it. The spores are also disseminated by *Drosophila* species, often being carried into the interior of broken fruit by ovipositing flies.

Another thing that was observed frequently is that the flies and parasites from *Mucor*-infested samples are visibly smaller than those from *Mucor*-free samples. At the end of the second experiment, all the adults which had not been damaged by molds or by handling were removed and dried to constant weight. The results (Table 18) indicated clearly that larvae developing in *Mucor* environments give rise to smaller adults than those which develop in other environments. It could probably be demonstrated that the influence of *Mucor* and other organisms noxious to the developing larvae extends even beyond reduced survival and reduced size. On the basis of experience with other insects, it would be reasonable to expect that flies and parasites bred in unfavorable media would also have shorter life spans and produce fewer eggs than those developing in more satisfactory surroundings.

TABLE 18. *Average weights (in milligrams) of flies and parasites emerging from* Mucor-*infested and* Mucor-*free samples in the 2nd experiment. Numbers in parentheses indicate number of specimens*

	Dacus dorsalis		*Opius oophilus*	
	Females	*Males*	*Females*	*Males*
Mucor-free	2.73 (7)	2.35 (8)	1.04 (37)	0.81 (17)
Mucor-infested	1.72 (5)	1.95 (2)	1.02 (16)	0.66 (5)

It is believed that *Mucor* is one of the most important biotic factors in the natural control of *Dacus dorsalis*. While it does not attack living larvae directly, it creates an extremely unfavorable larval environment which results in high mortalities and reduced size of larvae and adults. This 1 fungus alone is probably responsible for at least 1/2 of all the non-predator mortality observed in fruits on the ground.

Larval competition: One of the mortality factors mentioned in the

preceding section was the competition between larvae within the same fruit. The habitat of *Dacus dorsalis* is a greatly restricted one, for with only rare and insignificant exceptions, the host fruit in which a larva is hatched is the one in which it must either mature or die. It is therefore important to consider what effect crowding has on the survival of larvae in host fruits.

The number of larvae that can develop to maturity in any given fruit will depend upon a number of important variables; most notably (1) the size of the fruit, (2) the quality of the food, (3) the number of larvae which hatch from eggs laid in the fruit, that is, the initial infestation and (4) the condition under which the fruit is exposed in the field. The latter variable, in itself, is a most complex one, involving the factors of temperature, water, humidity, rate of decomposition, aeration of interior of fruit, exposure to predators, etc. While we have not attempted measurements of the influence of larval crowding under the highly variable conditions found in the field, 1 detailed experiment was carried out in the laboratory under conditions designed to be as near optimum as possible and with all major variables minimized, except for the initial larval infestation.

Fifteen uninfested yellow-ripe tree fruits were weighed individually and arranged in a series of increasing weight. The 5 lightest fruits were placed in group A, the 5 heaviest in group C, and the intermediates in group B. Five series of fruits were then made up from these 5 groups; each series containing 1 fruit from each of groups A, B and C, so that any variables associated with size would be randomized as well as possible. The average weights of the 5 series fell within the narrow range of 63.8 to 64.7 g per fruit. Each fruit in series A was then inoculated with recently hatched and unfed 1st instar larvae, the number of larvae being calculated to give an initial infestation of 0.2 larvae per gram of fruit. The initial infestations in the other series were controlled at 0.4, 0.8, 1.6 and 3.2 larvae per gram of fruit. A single fruit weighing 64.5 g was inoculated with 413 larvae, to extend the progression to the level of 6.4 1st instar larvae per gram of fruit. The fruits were plugged at 3 or more points and the larvae introduced into the holes so as to give them ample opportunity to become established. Each guava was placed in a syracuse dish which in turn was placed in a jar containing sand. The fruits were slashed to permit drainage of excess liquid which might drown the larvae and escaping immature larvae were returned to the fruit. As drying progressed the remaining fruit pulp and seeds were manipulated to conserve moisture. Everything possible, within the limits of the experiment, was done to achieve maximum survival. All fruits were kept at a constant temperature of 82 F, and *Drosophila* were excluded. The results are summarized in Fig. 12.

The influence of larval competition can be seen at even very light infestations. For every larva put into the 1st series of fruit, an average of only 0.54 adult flies emerged. In practical terms, this means that an av-

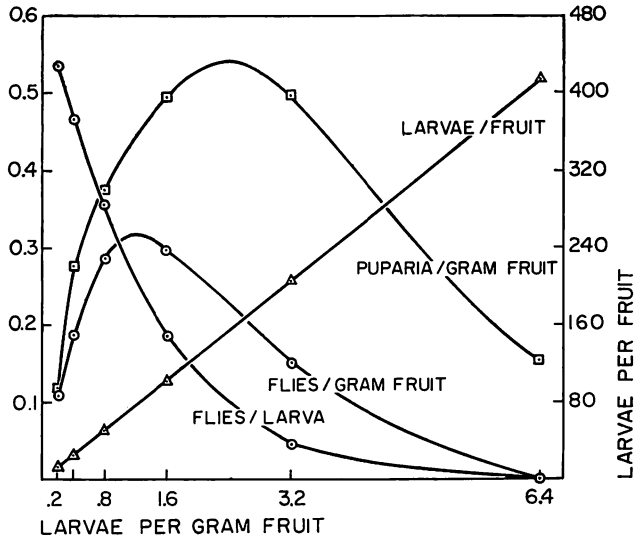

FIG. 12. *Relationship between initial infestation of fruit (larvae or eggs per gram of fruit) and survival in terms of adults reared per larva, puparia per gram of fruit, and adults per gram of fruit (use scale at left). The scale at right applies directly to the diagonal line (larvae per fruit), which in turn can be used to read the 3 curves in terms of larvae per average guava (about 64 grams).*

erage-sized[7] guava in which 13 viable eggs are laid, will produce 7 flies under optimum conditions. At all "oviposition" levels above this, the maximum yield/larva fell steadily, in the present experiment reaching a value of only 0.05 flies/larva (or viable egg) and a total of only 10 flies/fruit when 205 initially viable larvae/fruit were used. Production in terms of flies/larva or flies/gram of fruit reached zero at a point somewhere between 205 and 413 larvae/fruit. Maximum productivity (at about 20 flies/fruit) was reached at an infestation level between 0.8 and 1.6 1st-instar larvae/gram, or at a level equivalent to 80 viable eggs/fruit.

The influence of larval competition was also shown in the factor of pupal survival. Actually more pupae/gram were produced in those fruits with initial infestation levels between 1.6 and 3.2 1st-instar larvae/gram of fruit than at any other level. But these were obviously weaker than pupae produced at lower levels of initial infestation and yielded even fewer adult flies than did pupae from fruits which were inoculated with only 1/2 as many larvae. When 6.4 larvae/gram of fruit were used, only 2.5% of these produced pupae, all of which died.

The precise nature of the competition between larvae is not known, but there is no doubt about its reality. Presumably it is largely a matter

[7]The fruits collected at 60 stations over the island of Oahu in the first 9 months of 1953 averaged 62.5 g per fruit. For all practical purposes, then, the guavas used in this experiment were typical fruits, weighing an average of 64.1 g each.

of food supply, although modifying factors are probably associated with it. The significance of the factor will be considered further in the section on evaluation.

Rates of Parasitization: In a sense, the emergence of a parasite from a puparium represents pupal mortality. So far as the fruit fly population is concerned, the pupa is "dead"; in fact this is also strictly true, since development of the fly does not proceed beyond the stage of puparium formation. From July of 1950 through December 1953, the percentage of larvae parasitized was in excess of 65% in all but 3 months and averaged 74.5% for the 42 month period (Table 19).

TABLE 19. *Percentage of larvae parasitized, determined from total parasites and total flies reared each month from the fruit collection stations on Oahu*

	Jan.	*Feb.*	*Mar.*	*Apr.*	*May*	*June*	*July*	*Aug.*	*Sep.*	*Oct.*	*Nov.*	*Dec.*
1950	48.3	42.8	34.2	40.8	40.1	47.5	73.2	78.4	72.8	67.9	77.1	82.9
1951	91.4	72.3	68.7	69.0	78.0	81.3	81.3	78.7	85.2	79.6	71.3	91.9
1952	84.7	60.8	53.3	79.3	80.8	70.7	83.2	69.1	69.4	78.7	73.4	73.9
1953	77.5	72.2	63.9	66.0	70.0	78.8	68.2	57.0	76.0	75.0	70.1	69.0

Quarterly Averages

	Jan.-Mar.	Apr.-June	July-Sep.	Oct.-Dec.
1950	41.8	42.8	74.8	76.0
1951	77.5	76.1	81.7	80.9
1952	66.3	76.9	73.9	75.3
1953	71.2	71.6	67.1	71.4

Several points of interest are noticeable in the rates of parasitization. First of all is the abrupt change from rates below 50% to above 70%, which occurred from June to July in 1950. This is the time at which *Opius oophilus* became firmly established as the dominant parasite on Oahu. Second is the high average rate throughout 1951, followed by general decreases in 1952. Third is the apparent continuation of this trend in 1953. Whether the changes in sampling methods had anything to do with the lower level in 1953 cannot be stated for certain, but there is no reason to feel that they did. About the only way this could come about would be through a differential partitioning of parasitized larvae between those 1st dissected from the fruits and those recovered later and it is doubtful that this occurs to any significant extent.

In the section on egg mortality it was pointed out that a typical sample which yielded 75 *Opius oophilus* and 25 *Dacus dorsalis* would have been the survivers of a minimum of 500 eggs, of which 95% were parasitized and 80% died before hatching. The many thousands of individuals on which Table 19 is based must represent a fairly "typical sample," in which 74.5% of the puparia produced parasites. A study of Fig. 6 shows that when 75% of larvae are parasitized, we can estimate that this actually represents

a rate of about 95% true parasitization. The samples collected during 1951 and 1952 in the egg mortality studies averaged about this same value (76.2 % parasitization by rearing), and 94.3% of these eggs were parasitized. Hence the figure of 95% true parasitization must be a very close approximation of what transpired in the general population.

According to Fig. 6 we can further estimate that about 80% of the eggs in the population were killed before hatching. In the egg mortality studies, the overall mortality was only 75%, but as pointed out before, these contained a number of samples specifically selected because of their heavy infestations (hence hatch), so the figure of 75% is probably a little low. The generally good agreement between these estimates would appear to warrant considerable confidence in their reliability.

A word of warning is in order here, however, about using these relationships to estimate such variables as egg mortality and true % parasitization on the basis of observed rates of parasitization by rearing. The same degree of parasitization by rearing, say 75%, can be arrived at by many different paths. These range (theoretically) from 75% true parasitization by rearing at 0 mortality to 99.99+% true parasitization at 99.96 + % mortality. The chance that either of these extremes would be reached in a very large population is remote, of course, although the upper limit is certainly more nearly realized than the lower. Likewise, a rate of 50% parasitization by rearing is theoretically possible anywhere between 50% true parasitization at 0 mortality to 99.99+ at 99.98+ % mortality. These 2 examples should be adequate to point out that in small samples or groups of samples, or even many samples taken within a period of 1 or 2 months, it is not possible to make a reliable estimate of any of these other variables on the basis of % of parasitization by rearing.

To take a specific case, it is sometimes supposed that declining rates of emergence of *Opius oophilus* during the winter or early spring months (Table 19) was an indication of lessening effectiveness on the part of the parasite. A study of Table 10, however, shows that a more likely alternative lies in increased mortality rates of the parasitized eggs during November through January or even February. Such a change can and often does occur even without decreases in the relative ovipositional activity on the part of the parasite.

EVALUATION

In biological control, the term evaluation connotes an estimate of the importance of a given biotic factor either in reducing the abundance of a host species, or in holding in check a host already at an equilibrium population level. Several methods of evaluation are available, all of which come under one or more of the following general headings: (1) historical methods, (2) experimental methods and (3) inductive methods.

Historical methods are most satisfactory when a new factor is introduced

into a population which has already achieved a fairly stable equilibrium. Any significant and permanent change in the equilibrium level of the population may be attributed to the introduction of the new agent, provided no additional control factor was introduced at the same time. This might also be termed the "before-and-after" method.

Experimental methods should be satisfactory if applied on a large enough scale and under conditions which do not deviate too widely from normal. They are peculiarly subject to 1 type of error which must be guarded against at all times. Experimental control of a particular factor may actually produce secondary effects of greater importance to the population than the one which is being investigated, leading to false correlations between observed effects and presumed cause. Designing experiments which will significantly affect a single factor but leave all others totally unaffected is patently impossible. The objective must be to reduce these secondary effects to a level where they will not alter the essential validity of the conclusions.

Inductive methods require a very solid foundation of well-established facts, not only about the principal factors in question, but all others of subsidiary importance as well. While they may not have the incisiveness of a well-designed experimental approach, or the impressiveness of a significant and obvious reduction in a previously stabilized population, inductive methods can lead to fairly reliable conclusions. The fact that they require information on a wide variety of factors makes it possible to avoid some of the pitfalls of purely experimental or historical methods; and, of course, experimental or historical evidence can usually be drawn upon in any inductive approach to evaluation.

The decline in adult abundance from 1949 *to* 1951: So far as the specific case of *Dacus dorsalis* is concerned, strictly historical methods are of limited value because it is doubtful that the population density of this species had reached an equilibrium level at the time the various parasites and predators were introduced from other parts of the world. Therefore it is not possible to state that the great reduction in abundance of the oriental fruit fly was due solely to those introduced enemies. The earliest quantitative records we have are those of R. H. Van Zwaluwenburg of the Hawaiian Sugar Planters' Association, who has kindly given the authors permission to utilize the data. The basic data will not be presented here, but they show that the catch in his one standard-lure McPhail trap in Manoa Valley averaged 96.2 flies/day from April 1948 to March 1949 compared with 34.7 per day for the succeeding 12 months. This represents a drop of 64% in catch. During both of these periods, the maximum catches were recorded from October to March. The 1948–49 catches over the 6-month interval of maximum catch averaged 147.2 flies/day compared with 52.7 per day for the corresponding 6-month maximum in 1949–1950. This likewise gives a figure of 64% reduction the first year following the maximum

fruit fly population.

Kiyoshi Ito of the Pineapple Research Institute established a series of 10 traps along the windward side of the Waianae range in June 1948. These showed a somewhat more modest decline of about 35% from the 1948–1949 to the 1949–1950 season of peak fly catch. If we give equal weight to these 2 sources, then we would put the decline for this 1st year after the peak fly population at about 50%.

A further reduction occurred in 1950, although the magnitude of this is even less well documented than in the case of the 1949 decline, since Ito's traps were discontinued before the emergence of the fall crop of flies. However, his records do cover the 1st 1/2 of 1950 and the average catch over that period was only 48 to 50% as high as in the corresponding portion of the cycle of the previous year. The records from the single Van Zwaluwenburg trap continue through March 1951. From April 1950 through March, 1951, a period of one year, the catch averaged only 31% as high as during the preceding 12 months, indicating a drop of 69%. Thus while Ito's and Van Zwaluwenburg's traps were not in perfect agreement, they were consistent to the extent that both showed a somewhat higher drop in 1950 than in 1949. Again, if we give these 2 records equal weight, the adult population in 1950 was 59% below the 1949 population. Therefore, at the end of 1950, the population was roughly 20% of that of 1948, having undergone an 80% reduction over a period of 2 years.

Our own methyl eugenol traps were installed in June of 1950 in time to obtain a measure of the fall crop of flies of that year. From July of 1950 through June of 1951 the catch per day averaged 642 cc per day, while throughout the next 12 months the average was only 198 cc per day, indicating a reduction of approximately 70%.

When all of these estimates are combined, we find that the 1951–1952 population was only about 6% of the 1948–1949 population, indicating a drop of 94% within a 3 year period. Admittedly the data are not as good as would be desirable for the early part of the period, but even so, they appear to be quite representative. It is doubtful that many of those who watched the decline would deny that the oriental fruit fly was 5 times as abundant in 1948 as in 1950. Even laymen were very much aware of the marked decline within the one year of 1949 to 1950; and our records are fairly reliable from all standpoints for the decline from 1950 to 1951.

Since the low point of 1951 to 1952, the fly population has averaged about 25% higher than during that year; in other words, it now stands at about 7.5% of the 1948 level. This is assuming the figure of 6.0% as arrived at above to be essentially correct. This partial recovery of the population will be discussed again in a later section.

Factors involved in the initial decline of the population: The possible causes of the initial decline in infestation and the fly population appear to be at least 2 in number. In the first place, *Opius longicaudatus* was well estab-

lished by the last 1/2 of 1949 and even *Opius vandenboschi* was appearing in considerable numbers. From November 1949 through March 1950, at the peak of that season's fly catch, slightly more than 50% of the puparia collected by van den Bosch, Bess and Haramoto (1951) produced parasites. This by itself would be of about the right magnitude to explain the observed decrease in fly abundance from 1948 to 1949, assuming that the larval population was equal in these 2 years. In the 2nd place, it is possible that the drop in 1949 was due in part to larval competition in the fruits. It has already been shown that in 1951 and 1952, the number of eggs per fruit averaged 38.9 (34.1 in 1951 and 44.9 in the 1952 collections). These eggs were laid by a population which was only about 1/20th the size of the 1948 population, and if we assume that the oviposition rate per female in 1948 was equal to what it was in 1951–1952, then the fruits attacked by the 1948 crop of flies would have contained an average of about 800 eggs per guava fruit. It is certain that factors were operating in 1948 (e.g. competition for oviposition sites) which would result in figures for initial infestation levels of considerably fewer than 800 eggs/fruit; still it would not appear reasonable to reduce this by a factor of much more than 1/2, and even a factor of 3/4 would leave us with a seemingly conservative value of some 200 eggs/fruit. Experimental studies described above showed that maximum yields of adult flies were obtained at levels of about 80 hatched eggs/fruit. With the very low rate of egg mortality which is observed in the absence of *Opius oophilus*, this would mean no more than 85 eggs actually laid. The number of adult flies produced at 200 eggs/fruit would be only about 1/2 the number at 85 eggs/fruit, due to larval competition. While few of the factors that would be necessary to compute the expected decrease have been adequately measured, the margins of safety are so large that we can say with considerable assurance that it would have been a biological impossibility for the 1948 fly population to maintain itself at that level. Hence, we might surmise that after 1948 the population could have moved only in a downward direction until the very important effect of larval competition had been relieved. A population of the magnitude of that of 1948 could be produced only from 1 of smaller size.

Changes in infestation from 1949 *to* 1953: There is no immediately available record of infestation going back beyond November 1949 that can be compared very convincingly with data obtained subsequent to that time. Hence it is not possible to state definitely just what reduction in infestation occurred the 1st year or so after the introduction of parasites on Oahu. Generally speaking, there appears to have been a moderate reduction, but little more can be said. A rough estimate of the decrease in infestation following the establishment of *Opius oophilus* can be obtained by comparing the infestations over the 8-month period from November 1949 through June 1950 (Table 6). The infestation values over this interval were invariably higher than the values for the corresponding months in 1950,

1951 and 1952; in fact the "post-*oophilus*" values average only 26% of those obtained prior to the establishment of that parasite. This would indicate a reduction to about 1/4 of the level that existed prior to the time that this species replaced the others on Oahu. This is so near the figure for average egg hatch (24% in 175 samples, based on average of percentages) in the presence of *Opius oophilus* as to leave little doubt of the ability of egg mortality alone to account for the greater part of the decreased infestation, as well as for the parallel decrease in adult populations.

Coincident with the decrease in infestation, of course, was the increase in % of parasitization. During the 1st 1/2 of 1950, when *Opius vandenboschi* was the dominant parasite, the monthly rates of parasitization by rearing ranged from 34.2 to 48.3% and averaged only 42.3%. It is probable that the true rate was slightly higher than this, owing to mortality of some of the parasitized larvae. This would be comparable with the mortality of eggs resulting from bacterial infection. While no studies were made of larval mortality resulting from the attack of larval parasites, the contaminated environment in which *Dacus* larvae live would predispose the larval population to a certain amount of infection and subsequent mortality. However, the true rate of parasitization for the 1st 1/2 of 1950 was probably between 45 and 50%.

In the last 1/2 of 1950 and throughout 1951, the rate of parasitization by rearing averaged 77.8 or 1.8 times the previous rate. As shown in the section on egg mortality, such a rate leaves no reasonable doubt that the population was actually sustaining a true rate of parasitization of 97%—or more than double that of the first 6 months of 1950.

Returning to infestation, it should be pointed out that the upward trend in 1952 (Table 6) was correlated both with lowered rates of parasitization and with increased trap catches, hence is unquestionably real. As pointed out before, the very high value for 1953 was due more to a change in fruit sampling technique than to anything else. Still it is evident from other considerations that the average infestation for that year may have been somewhat higher than in 1952. Owing largely to drought, the relative fruit abundance in 1953 was about 16% lower than in 1952. Yet the fly population produced by the 1953 crop was only about 5% lower than in 1952. In other words, fewer fruits in 1953 yielded very nearly the same number of flies that were produced in 1952. The only way this could come about would be by way of a higher number of larvae/fruit, or possibly by somewhat better survival of the larvae that were present. About the latter possibility we can say very little, but the overall rate of parasitization in 1953 was down perceptibly from 1952, which would make for lowered egg mortality and subsequently a higher infestation.

Partial recovery from Opius oophilus: The 30-day methyl eugenol traps were installed at the end of June, 1950 which could be termed the last epidemic year for *Dacus dorsalis*. The average catch/day for the last half of 1950

was 1044 cc of flies. During the next 6 months, the catch averaged only 240 cc and was virtually the same for the last half of 1951 (Table 20). The lowest level reached during any 6 month period was in the 1st 1/2 of 1952, when the 11 traps combined caught only 154 cc of flies per day. First-half catches in both 1953 and 1954 were 45% and 21% higher than in 1952, despite the fact that the catches in the first few months of 1954 were still clearly reflecting the effect of the severe 1953 drought. Likewise, last-1/2 catches in both 1952 and 1953 were 16% to 18% higher than in 1951, and again the adult population in the latter part of 1953 was quite probably lower than it would have been under normal climatic and fruiting conditions.

TABLE 20. *Summary of trap catches by 6-month periods to show moderate increase in catch following low year of* 1951-1952. *Values show average cc of flies per day for 6-month periods. Basic data from Table* 5

	January-June	*July-December*
1950	—	1044
1951	240	241
1952	154	283
1953	223	280
1954	186	258

Considering the data by 12-month periods, the lowest overall catch was made from July, 1951 through June, 1952. Throughout these 12 months the catch averaged only 198 cc of flies per day. During the corresponding period of 1952–1953 the average catch was 253 cc or 28% higher. Even in 1953–1954, despite the consequences of severe drought, the catch was 18% higher than it was in 1951–1952. Each of these values is based on over 4000 trap-days, so there can be little doubt as to their general validity. There was, therefore, a distinct, although limited recovery of the adult population from the low point of 1951–1952.

Turning now to the data on parasitization (Table 19) we see that the highest rates were observed in 1951 when 79.1% of all larvae were parasitized. This long period of heavy parasitization led to the low adult populations of the last 1/2 of 1951 and early 1952. However, in November of 1951 and throughout the 1st quarter of 1952, the monthy rates of parasitization fell below the corresponding rates of the preceding year. At the same time, the rates of infestation exceeded the values for the corresponding months of the previous year. Considering what we know about the relationship between parasite activity and egg mortality, the most logical single explanation of these 3 phenomena—(1) the decrease in rates of parasitization in late 1951 and in 1952, (2) the corresponding increase in infestation and (3) the subsequent increase in trap catch beginning in the last half of 1952—is that there was a partial escape from the influence of *Opius oophilus*. It

would appear that the parasite in becoming established had overshot for a while the equilibrium level that it could maintain and that the partial subsidence of the rate of parasitization in 1952 reflected the adjustment to a more stable level of both abundance and relative ovipositional activity of the parasite. This overshooting is not to be compared with the cyclical changes in relative abundance of parasites (or predators) and their hosts frequently observed in established and mature populations, but is apparently a phenomenon peculiar to populations of recently introduced species. It is doubtful that *Opius oophilus* will ever again be as abundant as it was in 1951, or kill such a large % of the fly population as it did that year. In a way this is comparable with the overshooting of the equilibrium population level by *Dacus dorsalis* in 1948 when that species reached a level of abundance which would be next to impossible to maintain in a population of long standing.

The significance of egg mortality in evaluating the importance of Opius oophilus: The best single key we have in evaluating the importance of biological control in the case of *Dacus dorsalis* is the egg mortality produced by *Opius oophilus*. One highly significant inference that may be drawn from the data in the foregoing sections is that, in a population sustaining an average egg mortality of 80%, the instantaneous elimination of the parasite would be followed within 72 hours by an increase of 400% above the present infestation level! The combined samples collected during the course of the egg mortality studies produced an average of 7.4 larvae/fruit, but they also contained 38.0 eggs per fruit, virtually all of which would have hatched except for the activity of *Opius oophilus*. This great increase in 1 generation would continue into the 2nd generation before other factors could damp it.

An even more revealing consideration is the tremendous increase in production of *Dacus dorsalis* adults which would occur as a consequence of the instantaneous release of the population from *Opius oophilus*. In the section on rates of parasitization, it was shown that the true rate of parasitization which was sustained by the fruit fly population during 1951 and 1952 was very nearly 95%. Therefore, without the action of *Opius oophilus*, and assuming that no other parasites were operating, we could expect an increase in production of *Dacus dorsalis* of 19 times in the first generation. Other factors, including larval competition, would come into play to damp this increase somewhat, but these probably would not alter the results appreciably, at least at first. The increase could be expected to continue, although at a greatly reduced rate, into the 2nd, and possibly even 3rd generations. It should be apparent from a consideration of these figures that *Opius oophilus* alone is a most powerful factor in regulating the abundance of the oriental fruit fly, for an increase of about 14 times in the present fruit fly population would put it back at almost precisely its 1948 level, so far as the available data would indicate.

Ineffectiveness of predators as factors in reducing the fruit fly population: In evaluating the effect of the introduced natural enemies on the fruit fly population, it is necessary to consider if any increase in the effectiveness of the endemic predator fauna might have been induced by the large population of *Dacus dorsalis* in 1948. To begin with, all evidence points to the fact that no new predators of any significance have become established. The only important predators of *Dacus dorsalis* are those which were already in the islands at the time the fly was introduced. While it might be tempting to theorize that the once great larval population of *Dacus dorsalis* would have provided a base for an expanded ant population, this almost certainly was not the case. Life in a guava fruit is confining, to say the least, and the quantity of protein that can be derived from a given decomposing fruit must be fairly well fixed; whether this protein is in the form of microorganisms, larval drosophilids, souring beetles, *Ceratitis capitata*, or *Dacus dorsalis*. The competition between the elements of the biota is intense, hence the addition of *Dacus dorsalis* would not result in any increase in the biomass of insect protein available to the ant population, but only in a partial replacement of the other components, all of which are utilized by ants for food.

If the foregoing is true, and it is difficult to see how it could be otherwise, then there is no reason to believe that the ant population at the peak of abundance of *Dacus dorsalis* was any greater than it was before the oriental fruit fly first entered the islands. This is largely true for other predators as well, which are far less effective than ants in keeping the fly population in check.

This does not mean that predators play no part in keeping down the numbers of *Dacus dorsalis*, for it has been shown previously that where conditions for predator activity are favorable the predator population alone may account for as much as 40% to 60% of the larval and pupal population surviving mortality factors operating in the fruit. What it does mean is that we cannot explain any significant part of the great drop in the fruit fly population which occurred between 1948 and 1951 on the basis of increased predator-inflicted mortality. Hence we must look elsewhere for an explanation of the decrease in fruit fly abundance. It seems that the factors responsible must have been completely new to the fly population, and the only readily apparent possibilities are the opiine parasites introduced into Hawaii after *Dacus dorsalis* had reached epidemic proportions.

Egg mortality—good or bad?: If we return once more to the overall egg mortality rates observed throughout 1951 and 1952, we will find an interesting subject for speculation. Throughout that long period an average of 80% of all eggs laid by *Dacus dorsalis* on Oahu were killed through the activities of *Opius oophilus*. Very nearly 75% of the surviving eggs produced parasites, while the rest produced flies; in other words, 3 parasites emerged for every fly.

However, were it not for egg mortality, 5 of every 100 eggs would have

produced flies, but 95 would have yielded parasites, to give a ratio of not 3 : 1 but 19 : 1! Unfortunately we do not have the data to state specifically what effect this would have, but it is very obvious that 19 parasites would do a more thorough job of finding and parasitizing the eggs laid by a fruit fly than would 3, other things being equal. It is not possible, however, to state by what factor the searching capacity of the parasite population would be increased. Nevertheless it seems apparent that the % of eggs producing flies would be significantly reduced below its present level, and that the adult population would become stabilized at a lower level than it now enjoys. To that extent, egg mortality is an unfortunate development. For all practical purposes, egg mortality is parasite mortality.

One other point must be considered, however, namely the effect on infestation. A reduction in the adult population would be followed by a reduction in the egg population, and at low levels of abundance, these reductions would probably be very nearly proportional. For instance, reducing the present adult population by 1/2 would lead, in all likelihood, to a halving of the egg population. But virtually all of these eggs would hatch, with the result that the number of larvae per guava would be higher than at present, if we assume no further decrease in the adult population.

The question then becomes: Would the higher parasite/host ratio that would result from the elimination of egg mortality be sufficient to reduce the infestation level below its present magnitude? While we cannot say precisely what reduction in the adult population would be required to reduce the present infestation level, we could estimate that it would be of the order of 80% or more. Or to put it another way, a fly population only 1/5 as dense as our present one would be adequate to maintain the same level of infestation in guavas in the absence of egg mortality.

At the same time it should be remembered that a reduction of adult population to 1/5th of its present level might have some benefit, even though there might be no change whatever in the infestation in guavas. One of the most notable features about the decline in infestation by *Dacus dorsalis* is that not all host fruits were benefited equally. Some varieties of avocado, for example, were severely damaged by the fruit fly in 1948 and 1949, whereas today these same varieties are rarely attacked. Thus it is possible that marginal hosts might benefit from still further decreases in the adult population even though the infestation in guava remained the same.

These points are largely speculative, for there is nothing that can be done about egg mortality anyway, but they are of interest in evaluating the interaction of the host and parasite populations.

CONCLUSION

The data and conclusions presented here were arrived at in determining the influence of biotic factors on *Dacus dorsalis*. The work was undertaken primarily to evaluate the effectiveness of the parasites and predators

which were collected in various parts of the world, shipped to, bred and liberated in Hawaii, under the cooperative fruit fly research program.

The majority of these natural enemies failed to become established at all, or were recovered so sporadically and in such relatively small numbers that their contribution to the biological control of *Dacus dorsalis* can be ignored. Only 3 of these imported species, *Opius longicaudatus*, *O. vandenboschi.* and *O. oophilus* ever contributed materially to the biological control of *Dacus dorsalis.* The replacement of the 1st 2 by *O. oophilus* occurred in 2 steps, *O. vandenboschi* replacing *O. longicaudatus* as the principal parasite in September of 1949 (on Oahu) while *O. oophilus* exceeded the other 2 species in July 1950 and all succeeding months. After May 1951, *O. longicaudatus* and *O. vandenboschi* together have comprised considerably less than 5% of all parasites reared from guavas on Oahu.

Dacus dorsalis did not really make itself known on Oahu until 1946. Although it had increased tremendously by 1947, in view of what has been shown in the preceding pages about fruiting cycles in guava and the relationship to fly production, it is doubtful that the fly reached its all-time maximum until September or October of 1948.

The first liberations of *O. longicaudatus* and *O. vandenboschi* on Oahu were made by the Board of Agriculture and Forestry in July of 1948 and were continued for more than a year. The beginning of the decline of the fly population occurred between the fall of 1948 and that of 1949, or at a time when the fruit fly population definitely was coming under the influence of *Opius longicaudatus* and *O. vandenboschi.* The rates of parasitization in effect the last 1/2 of 1949 were adequate, or very nearly adequate, to account for the drop in fly population that occurred that year. Moreover, consideration of the probable level of egg production that could be expected from a population the size of that of 1948–1949 leads us to believe that larval competition would have been so intense that the production of flies would have been less in 1949 than in 1948, even in the total absence of parasites. Therefore it appears that the halving of the population observed in 1949 can be explained adequately on the basis of these 2 factors.

The drop from 1949 to 1950 appears to have been slightly greater; approximately 60%. Here 2 directly related factors were operating together. In the 1st place, larval infestation decreased, undoubtedly due to a great extent to the new factor of egg mortality also resulting from the activity of *Opius oophilus.* In the 2nd place, the percentage of larvae producing parasites increased considerably in the last 1/2 of 1950 when *Opius oophilus* became the dominant parasite. Both of these factors together are entirely adequate to account for the observed decrease.

The influence of these 2 factors continued into 1951, leading to the all-time low population of the 12-month period of July, 1951 to June, 1952. The reduction during that 1 year was about 70%. Here, again, it seems that the continued decline was due to these same 2 factors operating

together and that it is unnecessary to adduce any others to account for the observed decrease. At its lowest ebb, the fruit fly population was at about 6% of its former maximum abundance.

The slight increase in adult abundance which occurred in the year 1952–1953 was a very real thing, having its origin in a lower rate of parasitization, first observed in late 1951 and 1952. This increase was largely sustained in 1953–1954, despite the severe drought of 1953 which curtailed fruit production significantly. The observed phenomena agree well with the idea that the *Opius* population in 1951 had overshot its equilibrium level and that this was followed by a partial release of the fruit fly population from the influence of the parasite. After the 12-month low in 1951–1952, the fruit fly population averaged just 25% higher than it did during that year, and when this change is introduced into our calculations we would estimate the present population to be about 7 to 8% that of the 1948 epidemic year.

The best single key to the problem of evaluation is the factor of egg mortality. Field and laboratory studies showed that this is almost entirely due to microorganisms introduced by *Opius oophilus* and to traumatic injury by the parasite during oviposition. Studies in 1951 and 1952 indicated that 95% of the fly eggs laid in those years were parasitized, and that 80% of them died before they hatched. Instantaneous elimination of the parasites at that time would have resulted in a 4-fold increase in infestation, and a 19-fold increase in the number of larvae potentially producing flies. Since an increase of only about 14 times in the fly population would have put it back at the 1948 level, it is apparent that *Opius oophilus* alone is adequate to account for all of the reduction in fly abundance that had occurred at that time. What minor readjustments have taken place since 1952 would not alter this conclusion.

It is reasonable to ask if there are not factors which, with the sudden release of the fly population from the effects of the parasite, would come back into play to prevent an increase of 19 times in adult fly abundance. There is apparently only 1, namely larval competition. While this would most likely prevent the population from rebounding to a point 19 times above its 1951–1952 level, it probably would not keep it from regaining its former epidemic level, at least temporarily, after which we might expect it to drop somewhat.

The likelihood that there would be a significant compensatory increase in predator activity is remote, since the only predators which are at all effective in the natural control of *Dacus dorsalis* on Oahu are ones which were already here in 1946. Any increase in the biomass of *Dacus* would be compensated for by a decrease in the amount of available fruit and scavenger protein, so that there would be no net increase in food available to the predator population. This is not to say that predators, in particular ants, are not important in holding the fruit fly in check under

present conditions. Our studies indicate that 75 to 85% of the larvae present in fruits at the time they fall to the ground do not produce flies. The great majority (roughly 80%) of this mortality is due directly or indirectly to fruit decay, and predators probably account for between 40 and 60% of larvae and pupae which survive the other factors.

Most mortality in the larval and pupal stages stems from unfavorable conditions attending fruit breakdown. The fungus *Mucor* probably accounts indirectly for more individuals at this period of development than any other factor. Larval competition is important at high levels of infestation, and it is felt that this may have been a contributing factor in the 1st year of the decline of *Dacus dorsalis*. In laboratory studies the effects of competition are very marked at larval densities comparable with those which must have been current after the emergence of the 1948 crops of flies.

Host egg mortality has been shown to be a potent factor in limiting the population of *Opius oophilus*, since, for all practical purposes, every dead egg represents a dead parasite. Because of this parasite mortality, *Dacus dorsalis* at present probably enjoys a higher level of adult abundance than it would if there were no significant egg mortality.

In conclusion, it is felt that the decline of *Dacus dorsalis* on Oahu, as well as on the other islands, can be fully accounted for by the parasites introduced in the biological control program. In the early months this decline was probably aided to a limited extent by larval competition, but that factor was soon relieved. The present level of control of the oriental fruit fly, above and beyond that stemming from mortality factors already in operation in the earliest months of the outbreak, can be explained adequately by the control exerted by *Opius oophilus* and the other, now rare, opiines.

Whether the present degree of control amounts to economic control of *Dacus dorsalis* is somewhat outside the sphere of the present investigation. In some hosts, such as guava, it obviously does not; in certain marginal hosts which have seemingly been freed from economic damage by the great reduction in adult abundance, it appears reasonable to assume that it does. In between these 2 extremes it is evident that the reduction of the population has been great enough to permit effective use of cultural and chemical control measures which would have been quite impotent at the epidemic level of 1948.

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